Time Constraints of Breeding Twice. On the Fitness Relevance of Timing of Reproduction and Post-Fledging Parental Investment in the Barn Swallow (*Hirundo rustica*)

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GENERAL INTRODUCTION

Studying the intra-seasonal trade-off between successive broods

One of the major subjects of life-history theory is how an animal should allocate resources such as time and energy over its life in order to maximise lifetime fitness, and how differential survival in relation to these decisions shapes biological systems through selection (Roff 1992; Stearns 1992). From this evolutionary perspective, organisms in seasonal environments face a general trade-off between maximising their reproductive output within a season and maximising their survival to the next favourable breeding opportunity. In a seasonal environment, the optimal solution of this trade-off is likely to oscillate like a seesaw between reproduction and self-maintenance. The proximate processes of variation in life-history traits and selection by differential reproductive output are closely related to the seasonal variation in crucial ecological factors such as food resources or predation risk. The exact timing of reproduction can have strong effects on the organism's reproductive success and thus, fitness (McNamara et al. 1998; Houston et al. 1999). Selection is expected to shape the timing of the reproductive cycle and the associated physiological and behavioural mechanisms. Endogenous circannual rhythms provide the rigid basis for adaptive responses to periodically changing environmental conditions (Gwinner 1999). On the other hand, natural fluctuation in the ecological conditions require that organisms can respond flexibly to unpredictable variations by means of phenotypic plasticity (Hahn et al. 1997; Przybylo et al. 2000).

Quantifying costs and benefits of varying life-history traits and their impact on fitness in example biological systems is a crucial issue in life-history research. In birds, for example, selection in relation to reproductive decisions such as the timing of breeding is likely to operate after the young have left their nest, and eventually after migration to distant wintering sites. Often, nestling survival is very high but only a small proportion of juveniles finally recruit into the breeding population. As a consequence, concentrating research on a small part of the life cycle, e.g. on the pre-fledging period, will eventually miss the period when parents experience the rewards or retributions of their earlier decisions. This, in turn, hinders the understanding of mechanisms of life-history ecology and building of quantitative models. The five papers in this thesis use the barn swallow (*Hirundo rustica* L.) as an example organism and expand the insights into the reproductive ecology of this species by including the period after fledging. Only by considering this crucial part of the barn swallows' life cycle,

serious trade-offs become evident. The analyses show how individual variation in responding to these trade-offs results in differential reproductive output, and thus, in a feedback cycle that is an important, but so far ignored component of the life-history ecology of this species.

Double-broodedness

An animal can vary the number of young it produces in one season by altering either the number of young per breeding attempt or the number of breeding attempts per season (Stearns 1992). A wide range of bird species raises only one brood per year because the period of favourable ecological conditions is too short to permit later attempts. In contrast, many passerines raise more than one brood per year. In these species, the total seasonal fecundity largely depends on the number of breeding attempts (e.g. Bryant 1979; Geupel et al. 1990; Svensson 1995; Nagy et al. 2005a). A main determinant of the occurrence of multiple broods is the duration of the breeding season, which in turn is associated to the availability of food (Askenmo et al. 1986; Holmes et al. 1992; Morrison 1998). Hence, it is important to start reproduction early in the season because early breeding individuals are more likely to succeed with additional broods (Evans Ogden et al. 1996; Newton 1998). Therefore, in contrast to single-brooded species, multi-brooded species start the annual reproduction as soon as conditions permit the development of eggs (Crick et al. 1993; Svensson 1995). Later in the season, the onset of additional broods is only predicted when the expected benefits in terms of surviving chicks exceed the arising costs. In agreement with this, environmental conditions at the end of the breeding season determine whether birds invest in a next breeding attempt or in other functional processes such as migration (König et al. 1995; Jenni et al. 2003). To maximise the annual reproductive success, single-brooded birds face the problem to match the timing of their brood to the peak food availability (Van Noordwijk et al. 1995; Naef-Daenzer et al. 2001). In contrast, multi-brooded birds face more complex intra-seasonal trade-offs in the timing and the allocation of resources to the different breeding attempts (Nagy et al. 2005b). In particular, the fact that the period of favourable ecological conditions is relatively long does not imply that there are no time constraints for reproduction.

Post-fledging period

The ecological factors that determine a bird's survival prospect after leaving the nest are virtually unexplored, although the post-fledging period is considered a crucial bottleneck in avian reproduction because the juvenile mortality is high due to high predation rates (Anders

et al. 1997; Götmark 2002; Kershner et al. 2004). In several species, post-fledging survival strongly depends on the timing of the brood and the fledging condition of the chicks (Verboven et al. 1998; Brinkhof et al. 1997; Naef-Daenzer et al. 2001). Behavioural processes, for example in the context of parental investment or social interactions may play a decisive role in these post-fledging selection mechanisms (Edwards 1985; Nilsson 1990). Martin (1987) underlined that the post-fledging period is of crucial importance for understanding reproductive systems, and that there is hardly any evidence of the ecological mechanisms that affect post-fledging survival. Investigations of the post-fledging ecology of small birds have hitherto been hindered by the difficulties to track juvenile birds after fledging. Thus, the existing evidence is based on occasional visual observations of ringed birds. Approaches to quantify fledgling survival in natural populations focused mainly on the recruitment into the local study population. In recent years, advances in the miniaturization of radio-tags offered the opportunity to locate parents and fledglings of small bird species after leaving the nest (Naef-Daenzer 1994; Kenward 2001; Naef-Daenzer et al. 2005). In particular, radio-tracking allows the post-fledging survival of juveniles to be quantified with high accuracy and temporal resolution (Anders et al.1998; Vega Rivera et al. 2000; Naef-Daenzer et al. 2001). The present thesis makes extensive use of the new technical opportunities, and additionally includes experimentation to investigate crucial factors and parental decisions in the post-fledging part of the reproductive cycle.

Post-fledging parental care

The extent of parental investment is considered to be the outcome of trade-offs among fitness components (Clutton-Brock 1991; Székely et al. 1996; Westneat et al. 1996; McNamara et al. 2000). In altricial birds, parental care continues beyond fledging, including feeding and anti-predator behaviour. Various authors have discussed the duration and extent of post-fledging care as an important avian life-history trait. For example, tropical bird species differ from northern temperate species in that they lay smaller clutches, but provide more intensive post-fledging care (Martin 1996; Skutch 1996; Russell 2000; Russell et al. 2004; Schaefer et al. 2004). Also, cooperatively breeding birds (Langen 2000) and species breeding at higher elevations (Badyaev et al. 2001) provide prolonged parental care. Within species variation in the duration of parental care is reported from several avian species (e.g. Spear et al. 1986; Pöysä 1992; Cam et al. 2003; Wheelwright et al. 2003a; Yoda et al. 2004), including multi-brooded species, where parents are reported to provide longer care in final broods of the

season than between two subsequent broods (e.g. Edwards 1985; Geupel et al. 1990; Vega Rivera et al. 2000). Post-fledging care represents a parental investment in the period in which young birds must learn crucial life skills including effective foraging behaviour, predator vigilance and escape ability (Davies 1976; Marchetti et al. 1989; Wheelwright et al. 2003b). Investigations on the transition from parental feeding to offspring independence suggest that in passerines the timing of the end of this period is mainly under parental control (Davies 1976; Davies 1978). Although post-fledging care has been proposed to be an important life-history trait, studies on the costs and benefits of the varying extent of post-fledging care are almost lacking. In this thesis the period of post-fledging parental care is included in the study of parental breeding strategies and the costs and benefits of the varying duration of post-fledging care in the model species are investigated.

Trade-off between successive broods

Parental investment theory predicts that post-fledging care is expected to improve offspring survival, but also is traded against costs in terms of survival or future reproduction of the caregiver. Therefore, raising more than one brood per season may increase fitness only if the strategy, including the post-fledging investment, yields higher benefits compared to the alternative single-brood strategy (Boer-Hazewinkel 1987; Nur 1988; Smith & Marquiss 1995; Verhulst et al. 1996). From this perspective, parental strategies may also deviate from the optimal parental care in the 'point of view' of the offspring (Godfray 1995). High investment in one brood of the season also may entail costs in the subsequent brood because parents get physically or physiologically exhausted, leading to a trade-off between successive broods. In addition, time as a currency of trade-offs in parental effort may also be important (Kluyver et al. 1977; Verhulst et al. 1997). Prolonging parental investment beyond fledging is likely to increase the survival prospects of the brood, however, it also delays the start of the next breeding attempt towards the end of the season, resulting in costs in terms of offspring survival owing to the seasonal decline in environmental conditions (Svensson 1997; Nilsson 1999). The experiments presented in this thesis investigate in particular the trade-off between benefits from starting a subsequent clutch as soon as possible against costs from reduced survival of the first-brood chicks.

This thesis

Research goals

A main issue in behavioural and evolutionary ecology is to quantify the fitness relevant interactions between biological systems and their environment. To understand the evolution of reproductive systems, three main aspects require quantitative investigation: (1) the individual variation in important reproductive traits, (2) the underlying ecological mechanisms leading to variation in these traits, and (3) their fitness relevance in terms of differential survival and related selective processes. My PhD thesis is based on the general hypothesis that a double-brooded species breeding in a seasonal environment such as the barn swallow has to trade-off the benefits of prolonged parental care of the first brood fledglings against the benefits of an early start of the second brood. This hypothesis leads to three predictions that can be tested. First, the timing of second broods is fitness-relevant. Pairs can enhance the reproductive output of second broods by advancing the laying date (Prediction I). Second, the duration of post-fledging care is fitness-relevant. Pairs can enhance the reproductive output of first broods by prolonging the post-fledging care (Prediction II). Third, pairs that conduct a second brood stop investing in their first brood earlier than single-brooded pairs (Prediction III). Accordingly, parents are hypothesised to sacrifice a part of the fitness of their first brood in favour of the subsequent breeding attempts. I expect that double-brooded barn swallow pairs optimise the allocation of time to yield a net gain in the annual reproductive output compared to single-brooded pairs. The main aim of this thesis is to test the three predictions derived from the general hypothesis.

Model species barn swallow

As a facultative double-brooded species with a well-known breeding ecology the barn swallow (*Hirundo rustica* L.) is particularly suited to investigate the fitness relevance of the timing decisions and trade-offs outlined above. In Europe, 60–90 % of the pairs conduct two broods in a season and the overall breeding period covers 3–4 months (reviews in (Turner 2006)). Since barn swallows feed exclusively on aerial insects, weather conditions are important determinants of nestling condition and survival (Bryant et al. 1982; Turner 1982; Jones 1987a; Jones 1987b; de la Cueva et al. 1997).

Sexually selected traits, in particular the males' tail streamers, play a fundamental role for mating and reproductive success (Smith 1991; Møller 1994; Møller et al. 1998). The length of male tail streamers is a reliable signal for the bird's inherent quality, whereas evidence

points to tail length in females reflecting their body condition (review in Turner 2006). Barn swallows are long-distant migrants, with long-tailed individuals of both sexes arriving earlier at the breeding grounds and being more likely to conduct a second brood (Cuervo et al. 1996; Ninni et al. 2004; Møller 2004). In barn swallows, nestling mortality is low (review in Turner 2006). Therefore, it is probable that selection for crucial reproductive traits such as timing of breeding or nestling growth acts in the period from fledging to first breeding. Adult survival between breeding seasons is highly variable, but mostly under 50 % (review in Turner 2006). These low survival rates suggest that barn swallows should attempt to maximize the number of surviving offspring within a year rather than across years (Saether et al. 2000). Existing information from ring recoveries does not allow the post-fledging survival to be related to proximate ecological causes or to ultimate determinants. First-year survival has been estimated to some 30% (Siriwardena et al. 1998), but local recruitment of young birds has been reported as approximately 2% (Ferro et al. 1998). So far, it is therefore impossible to quantify the effects of parental breeding decisions or of environmental factors on juvenile survival, and consequently, to draw conclusions on the evolutionary mechanisms.

Outline of the thesis

In order to study the proposed trade-off between successive broods of barn swallows, the following main points were addressed. First, an appropriate (quantitative) measure of environmental quality and its variation over the breeding season was developed. In **chapter 1**, I present a model to estimate the spatio-temporal variation in the abundance of airborne insects on the basis of publicly available environmental data. This model estimates the average food availability in periods of interest, for example the post-fledging period, with good precision. This research allows a main ecological factor in the reproductive ecology of barn swallows to be included in all analyses.

Second, to quantify the fitness consequences of breeding decisions in the post-fledging period, I quantified juvenile survival as a response variable. To measure survival independently from visibility conditions I used Cormack-Jolly-Seber (CJS) mark-recapture models. This approach allows the separate estimation of re-encounter probability and survival probability on the basis of individual encounter histories. The resulting estimates of survival rates depend on the accuracy of the re-encounter model. **In chapter 2**, the methodological implications of estimating survival rates from radio-tracking data are addressed. The analyses of the effect of radiated power of radio-tags on the re-encounter probability of barn swallow

fledglings, and the evaluation of the performance of CJS-models in relation to sample size show that the methodological approach and the samples collected in the study allow post-fledging survival rates to be estimated with unprecedented accuracy and temporal resolution.

In **Chapter 3,** I test whether post-fledging survival of second brood chicks depends on the timing of the brood and whether it is associated with a seasonal deterioration in environmental conditions. Correlative studies on the fitness consequences of delaying the second brood face the problem that a seasonal decline in reproductive performance may be due to a decrease in the parental rearing competence rather than due to a decline in the quality of environmental conditions. To discriminate between these two hypotheses, and to quantify accurately the fitness costs of a delayed second brood (Prediction I), I conducted an experiment in which second clutches of early and late laying pairs were exchanged.

In **chapter 4,** I investigate the effects of variation in the duration of post-fledging care on post-fledging survival (Prediction II). I conducted a partial cross-fostering experiment with first broods, manipulating the duration of post-fledging care of fledglings within the same brood.

Based on records of the parental feedings during the post-fledging period, I analyze in **chapter 5** whether parent barn swallows adjust their post-fledging investment in relation to their subsequent breeding (Prediction III), and whether this change in investment is time- or state-dependent.

These five chapters form a case study of the ecological and evolutionary importance of a part of the barn swallow's reproductive system that has been largely ignored. Hence, the study contributes to closing an important gap. The thesis uses both natural and experimental variation in essential traits to build quantitative models, and thus, improves the understanding of the evolutionary ecology of the reproductive system of a uniquely suited example organism.

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SUMMARY

Time constraints of breeding twice. On the fitness relevance of timing of reproduction and post-fledging parental investment in the Barn Swallow (*Hirundo rustica*)

One of the major subjects of life-history theory is how an animal should allocate resources such as time and energy over its life in order to maximise lifetime fitness. Therefore, quantifying costs and benefits of varying life-history traits and their impact on fitness in biological systems is a crucial issue in life-history research. In seasonal environments, the exact timing of reproduction can have strong effects on the organism's reproductive success and thus, fitness. If conducting multiple breeding attempts, animals may be faced with complex intra-seasonal trade-offs in the timing of and the allocation of resources to the different attempts. Prolonging parental investment, for example, is likely to increase the offspring survival, however, it also delays the start of the next breeding attempt towards the end of the season, probably resulting in decreased offspring survival owing to adverse environmental conditions.

In many altricial birds, nestling mortality is low. Hence, selection in relation to reproductive decisions such as the timing of breeding is likely to operate after the young have left their nest. In addition, parental behaviour, for example in the context of parental investment, may play a decisive role for differential post-fledging selection mechanisms. However, investigations of the post-fledging ecology of small birds have hitherto been hindered by the difficulties to track juvenile birds after fledging. The present thesis makes use of new technical opportunities in radio-tracking, allowing the post-fledging survival to be quantified. Additionally, the studies include experimentation to investigate crucial factors and parental decisions in the post-fledging part of the reproductive cycle.

My PhD thesis is based on the general hypothesis that a double-brooded species breeding in a seasonal environment such as the barn swallow (*Hirundo rustica* L.) has to trade-off the benefits of an early start in the second brood against the costs of a reduced period of parental care in the first brood. This hypothesis leads to the following three predictions that can be tested and are the central subject of this thesis. (1) The timing of second broods is fitness-relevant (chapter 3). (2) The duration of post-fledging care is fitness-relevant (chapter 4). (3) Pairs that conduct a second brood stop investing in their first brood earlier than do single-brooded pairs (chapter 5).

In **chapter 1**, I developed an appropriate quantitative measure of environmental quality to investigate its variation over the breeding season. Flying insects represent the main source of food for the guilds of aerial insectivores and are an important ecological factor in the reproductive ecology of barn swallows. Based on a simple insect count technique, I present a model to estimate the spatio-temporal variation in the density of airborne insects from publicly available meteorological and habitat mapping data. The abundance of airborne insects depended largely on the daily weather conditions. Agricultural habitats differed considerably in the abundance of airborne insects, with peak insect numbers found along hedgerows and trees. The model quantifies the effect of weather conditions and agricultural land-use on aerial food webs in agri-environments. It allows the average food availability in periods of interest, for example the post-fledging period, to be estimated.

In **chapter 2**, I explored methodological aspects of estimating survival rates from radio-tracking data. Cormack-Jolly-Seber mark-recapture models estimate re-encounter probability and local survival on the basis of individual encounter histories. The resulting estimates of survival rates depend on the accuracy of the re-encounter model. I analysed the effect of radiated power of radio-tags on the re-encounter probability of barn swallow fledglings and I evaluated the performance of CJS-models in relation to sample size. In all types of radio-tags the re-encounter rates declined with time after leaving the nest. However, the slope of the decline was inversely related to the radiated power. Hence, the quality of radio-tags had a substantial impact on the probability to recover individuals and in turn, on the temporal resolution of survival estimates. The large samples collected in the study allowed post-fledging survival rates to be estimated with high accuracy. Sample size was also adequate to select complex survival models by AIC model selection.

Knowledge about seasonal variation in the fitness benefits of second broods is essential to understand the reproductive decisions in the first brood. In **chapter 3**, I investigated whether declining environmental conditions lead to a seasonal decline in the reproductive performance of second broods. Correlative studies on the fitness consequences of timing face the problem that a seasonal decline in reproductive performance may be due to a decrease in the parental rearing competence rather than due to a decline in the quality of environmental conditions. To discriminate between these two hypotheses, and to quantify accurately the fitness costs of a delayed second brood, I conducted an experiment in which second clutches of early and late laying pairs were exchanged, altering the parental timing of second broods. The mark-recapture models included estimates of food supply and the duration of post-fledging care. I

found a negative seasonal trend in offspring survival, the slope of which was associated with the seasonal variation in environmental conditions, i.e. food availability, but not with the seasonal variation in parental competence. Directional selection for early breeding occurred in the two years with scarce autumnal food supply. Furthermore, the results demonstrate a strong selection for long post-fledging parental care. Hence, the reproductive output of second broods was determined by two parental timing decisions: the timing of breeding and the duration of care.

In **chapter 4**, I tested experimentally whether the duration of post-fledging parental care affects post-fledging survival of first brood chicks. To disentangle the direct effect of post-fledging investment from pre-fledging effects, I conducted a partial cross-fostering experiment with first broods, manipulating the duration of post-fledging care of fledglings within the same brood. I found a strong effect of the duration of post-fledging parental care on both, the juvenile survival and its temporal variation. Long parental care improved offspring survival in the first 3 weeks post-fledging, and delayed and reduced the mortality peak after family break-up. Independent of the duration of care, juveniles originating from parents with high post-fledging investment had higher survival rates compared to chicks originating from short-care pairs. This component of variation in post-fledging survival was probably due to differences in the parents' efforts during the pre-fledging period. The results demonstrate that the duration of post-fledging parental investment is an important reproductive trait, accounting for a large proportion of differentials in post-fledging survival.

In **chapter 5**, I analysed whether parent barn swallows adjust their post-fledging investment if they conduct a subsequent breeding attempt, and whether the post-fledging investment depends on the timing, the body condition or the intrinsic quality of the pair. I showed that the duration of post-fledging care is reduced by 29 % in first broods compared to single and second broods. In second broods, the intensity of care in terms of feeding rates, but not the duration of care was increased compared to single broods. Furthermore, the period of post-fledging care was reduced in pairs breeding late and in pairs with long-tailed females. These results are consistent with the hypothesis of an intra-seasonal trade-off in the allocation of time between successive broods.

The thesis investigates a so far ignored part of the reproductive system of the barn swallow. I used a novel approach by considering behavioural mechanisms and selective processes of the post-fledging period. The fitness relevance of timing and duration of post-fledging care indicate that time is an important currency of parental investment. The results are

consistent with all three predictions of the general hypothesis. Thus, I conclude that barn swallows face a strong intra-seasonal trade-off in the allocation of their efforts to their broods: Parent barn swallows sacrifice a part of the output of their first brood, thereby increasing the output of their subsequent breeding attempt by an earlier timing. Estimates of the annual reproductive output demonstrate that double-brooded barn swallow pairs optimise the allocation of time to yield a net gain in the annual reproductive output. Hence, in multi-brooded altricial species, the timing of family break-up is an adaptive reproductive decision maximising lifetime reproductive output. In conclusion, this thesis demonstrates that extending investigations of avian reproductive systems beyond fledging reveals exciting new insights into life history evolution and behavioural ecology, even of well-known example species. Hence, the study contributes to understanding reproductive systems as well as the evolutionary processes shaping them.

ZUSAMMENFASSUNG

Zeitprobleme bei zwei Jahresbruten: Auswirkungen des Brutzeitpunkts und der Flügglingsbetreuung auf die Fitness bei Rauchschwalben (*Hirundo rustica*)

Eine der zentralen Fragen der Life-history-Theorie ist, auf welche Weise ein Tier Ressourcen wie Zeit und Energie im Verlauf seines Lebens einsetzen muss, um seine biologische Fitness zu maximieren. Die quantitative Bestimmung der Kosten und Nutzen von variierenden Merkmalen im Leben von Organismen ist deshalb eine entscheidende Angelegenheit in der biologischen Forschung. Bei Vögeln, die in einem saisonalen Umfeld brüten, kann etwa der Zeitpunkt des Brutbeginns einen starken Einfluss auf den Fortpflanzungserfolg und deshalb auch auf die Fitness haben. Arten mit mehreren Jahresbruten müssen komplexe Kompromisse in der Aufteilung des Betreuungsaufwandes auf die verschiedenen Bruten eingehen. Eine längere Betreuung der ersten Brut kann etwa deren Überlebenschancen erhöhen, doch gleichzeitig verzögert sich der Start der nächsten Brut. Dies wiederum kann die Überlebenschancen der nächsten Brut schmälern, weil sich die Umweltbedingungen gegen Ende der Brutsaison verschlechtern.

Bei vielen Nesthockern mit geschützten Nestern ist die Nestlingsmortalität gering. Selektion in Bezug auf Fortpflanzungsentscheidungen, wie zum Beispiel den Brutzeitpunkt, findet deshalb erst nach dem Ausfliegen der Nestlinge statt. Zusätzlich kann das Verhalten der Eltern, etwa die Intensität und Dauer der Betreuung der Flügglinge, eine entscheidende Rolle in den Selektionsmechanismen nach dem Ausfliegen spielen. Die Ökologie kleiner Vogelarten nach dem Ausfliegen wurde bis anhin aber kaum untersucht, da es mit den vorhandenen Methoden schwierig war, die flüggen Jungvögel zu verfolgen. Die vorliegende Dissertation macht Gebrauch von neuen technischen Möglichkeiten in der Radiotelemetrie, die es erlauben, das Überleben von Flügglingen zu quantifizieren. Zusätzlich werden Experimente einbezogen, um kritische Faktoren und elterliche Entscheidungen in der Zeit nach dem Ausfliegen zu untersuchen.

Meine Dissertation basiert auf der Grundhypothese, dass eine zweibrutige, in einer saisonalen Umwelt brütende Vogelart wie die Rauschschwalbe (*Hirundo rustica* L.) abwägen muss zwischen dem Nutzen, der durch eine frühe Zweitbrut entsteht, und den Kosten, die bei der Erstbrut durch eine verkürzte Betreuungsdauer entstehen. Diese Hypothese macht folgende drei Vorhersagen, die geprüft werden können und die hier anhand der Rauchschwalbe zentral

behandelt werden. (1) Der Zeitpunkt einer Zweitbrut ist relevant für deren Bruterfolg (Kapitel 3). (2) Die Betreuungsdauer der Flügglinge ist relevant für den Bruterfolg (Kapitel 4). (3) Brutpaare, die eine Zweitbrut beginnen, beenden die Betreuung der Erstbrut-Flügglinge früher als Brutpaare mit nur einer Jahresbrut (Kapitel 5).

Im **ersten Kapitel** meiner Dissertation entwickelte ich ein adäquates Maß für die Umweltqualität von Rauchschwalben, um brutzeitlichen Schwankungen der Umwelt in den Auswertungen berücksichtigen zu können. Fliegende Insekten sind die Hauptnahrung der Gilde der Luft-Insektenfresser und sie sind ein wichtiger Faktor in der Fortpflanzungsökologie der Rauchschwalbe. Ich präsentiere ein Modell, das auf Daten einer einfachen Insektenzählmethode beruht und das erlaubt, die räumliche und zeitliche Variation in der Fluginsektendichte aus öffentlich erhältlichen Wetterdaten und Kartierungen zu berechnen. Die Menge der Fluginsekten war weitgehend abhängig von den Wetterbedingungen des Tages. Landwirtschaftliche Habitate unterschieden sich stark in der Insektendichte. Entlang Hecken und an Einzelbäumen wurden die höchsten Dichte-Werte festgestellt. Das Modell quantifiziert den Einfluss von Wetterbedingungen und landwirtschaftlicher Nutzung auf die Nahrungsnetze in der Luft. Es erlaubt, das mittlere Nahrungsangebot für Zeitperioden wie z. B. die Flügglingszeit zu berechnen.

Im **zweiten Kapitel** erforschte ich methodologische Aspekte der Berechnung von Überlebensraten aus Radiotelemetriedaten. Cormack-Jolly-Seber (CJS) Fang-Wiederfang Modelle berechnen Wiederantreff-Wahrscheinlichkeit und Überlebensraten auf der Basis von individuellen Wiederbeobachtungs-Geschichten. Die berechneten Überlebensraten sind abhängig von der Genauigkeit der Modellierung der Wiederantreff-Wahrscheinlichkeit. Ich untersuchte den Effekt der abgestrahlten Leistung der benutzten Radiosender auf die Wiederantreff-Wahrscheinlichkeit von Rauchschwalben-Flügglingen und ich beurteilte das Ergebnis der CJS-Modelle in Abhängigkeit der Stichprobengrösse. Bei allen Typen von Radiosendern nahm die Wiederbeobachtungs-Wahrscheinlichkeit mit der Zeit nach dem Ausfliegen ab. Die Steigung der Abnahme war umgekehrt proportional zu der abgestrahlten Leistung. Folglich hatte die Qualität des Radiosenders beträchtlichen Einfluss auf die Wahrscheinlichkeit, Flügglinge wieder aufzufinden, und auf die zeitliche Auflösung der Überlebensschätzungen. Die Stichproben, die in dieser Dissertation verwendet wurden, erlauben eine präzise Schätzung der Überlebensraten von Flügglingen und waren genügend gross, um auch komplexe Überlebensmodelle mittels AIC-Modellauswahl zu selektieren.

Die Kenntnis von saisonalen Unterschieden im Fortpflanzungserfolg der Zweitbrut ist entscheidend für das Verständnis von Fortpflanzungs-Entscheidungen in der Erstbrut. Im **dritten Kapitel** untersuchte ich deshalb, ob die sich gegen Ende der Brutsaison verschlechternden Umweltbedingungen bei Zweitbruten zu einer saisonalen Abnahme der Überlebenschancen von Flügglingen führen. Korrelative Untersuchungen über Fitness-Auswirkungen des Brutzeitpunkts haben den Nachteil, dass die saisonale Abnahme vielleicht eher durch eine Abnahme in der Elternqualität zustande kommt als durch eine Verschlechterung der Umweltbedingungen. Um zwischen diesen beiden Hypothesen zu unterscheiden und um die Kosten einer verspäteten Zweitbrut quantifizieren zu können, führte ich ein Experiment durch, in dem Zweitbruten von früh bzw. spät legenden Brutpaaren ausgetauscht wurden. Damit änderte sich für die Brutvögel der Zeitpunkt des Brutgeschäfts. Die Fang-Wiederfang-Modelle berücksichtigten auch das Nahrungsangebot und die Betreuungsdauer nach dem Ausfliegen. So konnte ich zeigen, dass für das schlechte Überleben von späten Zweitbruten nicht die Elternqualität, sondern tatsächlich die Umweltbedingungen verantwortlich waren. Die saisonale Abnahme der Überlebenswahrscheinlichkeit von Flügglingen war in den verschiedenen Jahren unterschiedlich stark ausgeprägt. Dies lag am jährlich unterschiedlichen Nahrungsangebot. Selektion für einen frühen Start der Zweitbrut konnte ich nur in den zwei Jahren feststellen, in denen das Nahrungsangebot im Lauf des Sommers besonders stark zurückging. Darüber hinaus zeigten die Resultate eine starke Selektion für eine lange Betreuungsdauer von Flügglingen. Der Fortpflanzungserfolg von Zweitbruten wurde also durch zwei zeitliche Entscheidungen der Eltern bestimmt, nämlich durch den Zeitpunkt der Eiablage und die Betreuungsdauer nach dem Ausfliegen.

Im **vierten Kapitel** untersuchte ich experimentell, ob die Betreuungsdauer nach dem Ausfliegen das Überleben von Flügglingen beeinflusst. Damit ich den direkten Einfluss der Betreuungsdauer nach dem Ausfliegen von Einflüssen aus der Zeit vor dem Ausfliegen unterscheiden konnte, führte ich ein Experiment bei Erstbruten durch, bei dem gleichzeitige Bruten zur Hälfte ausgetauscht wurden. Dies führte dazu, dass Jungvögel aus der gleichen Brut nach dem Ausfliegen unterschiedlich lange betreut wurden. Die Betreuungsdauer hatte einen starken Einfluss auf das Überleben der Flügglinge und auf die zeitliche Entwicklung der Überlebensraten. Eine lange Betreuungsdauer verbesserte das Überleben der jungen Rauchschwalben in den ersten 3 Wochen nach dem Ausfliegen. Bei langer Betreuung wurde das Mortalitätsmaximum, das bei Rauchschwalben kurz nach der Auflösung der Familien auftritt, verzögert und abgeschwächt. Unabhängig von der Betreuungsdauer überlebten

Flügglinge aus Bruten von lang betreuenden Eltern besser als Flügglinge aus Bruten von kurz betreuenden. Dieser Unterschied im Überleben der Flügglinge beruhte wohl auf Unterschieden im Investment der Eltern vor dem Ausfliegen der Brut. Die Resultate zeigen, dass die elterliche Betreuungsdauer ein wichtiges Fortpflanzungsmerkmal ist, das einen großen Anteil der Unterschiede im Überleben von Flügglingen erklärt.

Im **fünften Kapitel** untersuchte ich, von welchen Faktoren Rauchschwalben-Eltern das Ende der Betreuung abhängig machen, nämlich, ob sie das Ausmaß ihrer Betreuung an das Auftreten einer Folgebrut anpassen und ob die Betreuungsdauer vom Zeitpunkt der Erstbrut und vom Zustand der Eltern abhängt. Die Betreuungsdauer von Erstbruten war im Vergleich zu Einzel- und Zweitbruten um 29 % verkürzt. Die Fütterungsraten von Zweitbruten waren aber höher als in Erst- und Einzelbruten. Außerdem war die Betreuungsdauer in Brutpaaren, die spät mit der Erstbrut starteten, und in Brutpaaren mit Weibchen von hoher Kondition verkürzt. Die Resultate stimmen mit der Hypothese überein, dass die Aufteilung der zur Verfügung stehenden Zeit auf verschiedene Bruten ein wichtiges Merkmal von Brutstrategien ist.

Die vorliegende Dissertation erforscht das Fortpflanzungssystem von Rauchschwalben. Dabei wurden neu Verhaltensmechanismen und selektive Prozesse der Flügglingszeit berücksichtigt. Die Auswirkungen von Brutzeitpunkt und Betreuungsdauer auf den Bruterfolg weisen darauf hin, dass Zeit bei der Investition in eine Brut eine wichtige Währung ist. Die Resultate bestätigten alle drei Vorhersagen der Grundhypothese. Dies zeigt, dass Rauchschwalben-Eltern bei der Verteilung der verfügbaren Zeit auf zwei Bruten einen Kompromiss eingehen. Sie opfern einen Teil des Bruterfolges in der Erstbrut, um den Bruterfolg in der Zweitbrut durch einen frühen Start erhöhen zu können. Schätzungen des Jahresbruterfolges zeigten auf, dass zweibrutige Paare die verfügbare Zeit so auf die beiden Bruten verteilen, dass am Ende des Jahres ein Gewinn resultiert. Der Zeitpunkt der Familienauflösung ist deshalb bei Nesthockern, die mehrmals im Jahr reproduzieren, eine adaptive Entscheidung der Eltern, die den lebenslänglichen Bruterfolg maximiert. Diese Dissertation demonstriert, dass die Ausdehnung der Erforschung von Fortpflanzungssystemen bei Vögeln auf die Zeit nach dem Ausfliegen spannende neue Einblicke in die Life-history-Evolution und die Verhaltensökologie sogar von gut bekannten Arten ergibt. Die Untersuchung trägt deshalb zum besseren Verständnis von Fortpflanzungssystemen und deren Evolution bei.

CHAPTER 1

A predictive model of the density of airborne insects in agricultural environments

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Abstract

Airborne insects in agricultural landscapes includes numerous beneficial and pest species, and disease vectors. Furthermore, flying insects represent the main source of food for the guilds of aerial and perching insectivores. Although of considerable economical and ecological concern, the temporal and spatial variation in the abundance of airborne insects are poorly understood. We present a model to predict the daily spatio-temporal variation in the abundance of airborne insects on the basis of publicly available environmental data. The validation of the model using extra data revealed a high correspondence between predicted and observed insect density. The final model showed that the abundance of airborne insects depended largely on the daily weather conditions. Agricultural habitats differed in the abundance of airborne insects, with peak insect numbers found along hedgerows and trees. This accumulation pattern was most pronounced at low temperatures and in windy conditions. Efforts to enhance insect abundance in agricultural landscapes therefore need to increase the number of woody structures. The model determines the effects of weather and agricultural land-use on aerial food webs in agri-environments on the basis of meteorological and habitat mapping data. It allows the abundance of airborne insects to be estimated for different periods or spatial research units. This gives manifold opportunities for quantitative comparisons of periods differing in weather conditions and areas differing in habitat composition, including analyses of effects of climate change and of changes in agricultural landscape structure.

1. Introduction

Flying arthropods in agricultural landscapes are of ecological and economical concern, because they include numerous pest organisms and vectors of diseases (e.g. Balashov, 1984; Hill, 1997; Goulson et al., 2005). On the other hand, many airborne insect species serve as pollinators of cultivated plants (Kearns et al., 1998) or as natural enemies of harmful species (Landis et al., 2000). Furthermore, flying arthropods represent the main source of food for the guild of aerial and perching insectivores, such as birds and bats. The spatio-temporal variation in the abundance of airborne insects affects the population density and behaviour of these predators, since variation in food supply influences all aspects of their biology (Kunz, 1982; Martin, 1987). In turn, aerial insectivores reduce insect pests (Kirk et al., 1996; Lee et al., 2005).

The abundance of arthropods in the air is mainly influenced by their flight activity in response to weather conditions (Taylor, 1963; Lewis, 1965, 1967; Johnson, 1969; Pedgley, 1982; Pedgley, 1990; Peng and Sutton, 1992; Poulsen, 1996) and by their habitat selection within the agricultural landscape (Lewis, 1970; Pasek, 1988; Ryszkowski et al., 1991; Söderström et al., 2001). However, existing studies on insect abundances near ground level are often restricted to selected taxa, whereas little is known on the spatio-temporal patterns in the total abundance of airborne insects (for high-altitude flight activity of insects see Smith et al., 2000; Chapman et al., 2002).

Several avian studies have quantified the impact of weather conditions and agricultural habitat structure on the abundance of flying insects (Bryant, 1975; Turner, 1982; Jones, 1987; McCarty and Winkler, 1999; Møller, 2001). However, these approaches were limited in either the temporal or spatial resolution due to the high sampling effort required in monitoring insect abundances. For example, suction traps were chosen to record the temporal variation in insect abundance at selected sites, whereas sweep-netting was frequently used to quantify spatial variation. So far, the enormous sampling and handling effort handicapped the monitoring of insect abundance over both large areas and long periods.

Recent climate change advanced the annual occurrence of airborne insects as a consequence of changing weather conditions, such as increased spring temperatures (Fleming and Tatchell, 1995; Roy et al., 2001; Goulson et al., 2005). Furthermore, the length of the growing season and, thus, the period of high insect flight activity has been extended in the late summer (Menzel and Fabian, 1999). Both changes might lead to prolonged pest exposure and altered breeding strategies of aerial insectivores (Saino et al., 2004). On the other hand,

changes in agricultural land-use and landscape composition might influence the abundance and the biodiversity of above-ground arthropods (Duelli et al., 1999; Dauber et al., 2005; Schweiger et al., 2005) and therefore affect the breeding and foraging biology of birds (Bruun and Smith, 2003) and their population sizes (Siriwardena et al., 1998; Chamberlain et al., 2000). Modelling the temporal and spatial dynamics of airborne insects therefore provides a useful tool in predicting the accumulation patterns of flying beneficial and pest species in changing weather conditions and in changing agricultural landscapes, and in estimating the corresponding food consequences for aerial and perching insectivores.

Herein, we analyse the abundance of airborne insects in relation to weather conditions and to the various habitat types in agricultural landscapes throughout the vegetation period. We build a model predicting the daily insect abundance patterns on the basis of publicly available meteorological and agricultural information. We validate this model using independent data.

2. Materials and methods

2.1. Counting insects

Flaspohler (1998) presented a technique that allows the temporal and spatial variation in the abundance of airborne insects to be quantified with minimal effort. The insects are counted using binoculars as they cross a defined area during a fixed time interval. We adapted this method to quantify the abundance of insects in the lowest layer of air above the vegetation. We mounted a white board (0.7 m x 0.5 m) about 0.1 m above the vegetation of fields and close to structural elements such as hedgerows, single trees or orchards (0.1 m from the outermost twigs). We counted the insects that crossed the board for a period of 3 minutes. The counts were made from a 10 m distance with binoculars (10 x 42). Insects with a body length of more than 1.5 mm were always detectable if they moved within the field of focus, i.e. 4.2 m from the white board. Small insects such as tiny Diptera and aphid species were underestimated due to difficulties in detectability. Thus, we counted insects passing a volume of c. 1 m^3 air in front of the board (for tests of detectability see Flaspohler, 1998). Data were collected between May and September in 4 farmland areas in different regions of Switzerland: Riviera (46°15'N 9°02'E; southern Switzerland; 240 m a.s.l.; year 2001), Vaulruz (46°37'N 6°59'E; western Switzerland; 820 m a.s.l.; year 2001), Pays d'Enhaut (46°27'N 7°08'E; western Switzerland; from 920 m to 1450 m a.s.l.; year 2001), Wauwilermoos (47°10'N 8°02'E; central Switzerland; 520 m a.s.l.; years 1999 to 2003). Thus, insect counts are

available from farmland regions both north and south of the Alps and from altitudes ranging from 240 m to 1450 m a.s.l. Insects were counted at different agricultural habitat types. These were classified as arable land (without cereal, e.g. root crops, potatoes, maize), cereal (wheat, barley), grassland (ungrazed meadows), cattle pasture (grazed) and structural elements of the landscape (hedgerows, single trees, orchards). Two to 15 daily counts per habitat type were recorded (mean: 3.94 ± 3.5 SD; Table 1). The daily counts were evenly distributed over the day, from 7 am to 7 pm. In 1999 and 2002–2003 sampling locations were selected randomly around different farms in the Wauwilermoos area (1999: 110 locations; 2002: 40 locations; 2003: 22 locations). In 2000–2001 we installed fixed sampling locations in the different habitat types (2000: 5 habitat types, 10 locations; 2001: in each sampling region 4–12 locations of the two habitat types "grassland" and "structural elements"). In the Wauwilermoos area, the counts were made twice a day (morning and afternoon). We built the predictive model using the counts from 1999 and 2000 in the Wauwilermoos area. In a second step, the model was validated using the data collected in the same region but in the subsequent years, 2001 to 2003. The data from the other regions (collected only in 2001) were used to test for differences between regions and altitudes (Table 1).

2.2. Meteorological data

Meteorological data used in the modelling and model validation represented arithmetic means (temperature in °C, wind speed in m/s) and sums (precipitation in 0.1 mm, sunshine in minutes) over 15 daylight hours (from 4.40 h to 19.40 h UTC = 6.40 h to 21.40 h; Swiss summertime) from the meteorological station Buchs-Suhr (47°23'N 8°05'E; MeteoSchweiz: Klimadienste, Zürich, Switzerland). In 2001, when counting in different regions and at different altitudes, we recorded meteorological data at a local scale by measuring the temperature with a hand-held electronic thermometer and by scoring rain intensity, wind speed and sunshine intensity during the 3-minute insect counts. The daily means of these local data were used to test for differences in insect numbers in the different regions and altitudes.

2.3. Statistical analysis

Model: We built a quantitative model on the basis of the insect count data from the Wauwilermoos area (1999–2000) using General Linear Model analysis and the daily average of counts for each habitat type as response variable. Counts showed a skewed distribution (skewed right). Therefore, to obtain a two-tailed data distribution, count data (means of insect

numbers $(3\ min)^{-1}\ m^{-3}$) were ln-transformed (ln(counts + 1)). Sample sizes are given in Table 1. As predictors, we included the meteorological variables and, to account for seasonal changes, the relative day length. Furthermore, the square term of the meteorological variables (non-linear relationships) and their two-way interactions were included into the set of predictors. The factor habitat type and the two-way interactions between habitat type and the meteorological variables were used to expand the meteorological results into space. Model selection was based on Akaike Information Criterion (AICc) (Burnham and Anderson, 1998), where the model with the lowest AICc-value is the most parsimonious. To avoid building of an unreasonably large number of candidate models, we refrained to build models with higher order interactions and built the model in two steps. First, we built only models at the basis of the seasonal and meteorological variables (including square terms and interactions) and selected the most parsimonious model. Second, the best meteorological model was extended by including the habitat types and their interactions with meteorological variables. Analyses of the residuals from the best-ranked model confirmed that this approach did not violate any basic requirements of GLM (normally distributed residuals: Kolmogorov-Smirnov statistic = 0.024; df = 766; p = 0.20; homogeneity of variances: Levene's test: $F_{4,761} = 2.165$, p = 0.071; multicollinearity: levels of intercorrelation among predictors: all r < 0.605).

The fixed sampling protocol in 2000 (fixed stations, fixed effort) allowed testing for autocorrelation of successive daily counts at the same sites. The autocorrelation function of the residuals of the best model was investigated by building time series either using the daily mean residuals (averaged values of the 5 habitat types) or using the residuals of the 5 habitat types separately. Neither the daily mean residuals (autocorr = 0.058 ± 0.094 SE, Box-Ljung = 0.38, p = 0.54, n = 110), nor the separate residual time series of the habitat types were temporally autocorrelated (arable land: autocorr = 0.101 ± 0.094 SE, Box-Ljung = 1.16, p = 0.28; cereal: autocorr = 0.187 ± 0.112 SE, Box-Ljung = 2.80, p = 0.09; grassland: autocorr = -0.025 ± 0.094 SE, Box-Ljung = 0.07, p = 0.79; pasture: autocorr = 0.145 ± 0.094 SE, Box-Ljung = 2.36, p = 0.12; structural elements: autocorr = 0.178 ± 0.094 SE, Box-Ljung = 3.59, p = 0.06). The lack of significant autocorrelation functions confirms that treating daily mean counts as statistical units was adequate.

Model validation: The predicted values for the Wauwilermoos area (2001–2003), calculated using the model (1999–2000), were compared to the observed values (2001–2003) by linear regression (for data sets, see Table 1). We tested whether the slope and the intercept of the resulting regression line differed from the expected equality function (i.e. slope = 1.0;

intercept = 0.0). As additional measurements of correspondence between observed and predicted values, we used (1) the root mean square error (rsme) and the Pearson correlation (r) between observed and predicted values, (2) the shrinkage, which is defined as the difference between the original R^2 (i.e. the model using the basic data set) and the new R^2 of the testing sample (i.e. the regression of the validation data set on the predicted values; Osborne, 2000), and (3) the validation method proposed by Kleijnen et al. (1998). This method tests, if the predicted and the observed values have the same mean and the same variance by regressing the difference between observed and predicted values against the sum of their values. If the model is accurate, there is no significant relationship.

Regions: Insect flight activity might differ between regions. Thus, the daily means of insect abundance (calculated from at least two counts at two different locations of the same habitat type) in different regions were used to test for between-region differences and for the within-region effect of altitude (GLM, controlling for local meteorological variables and habitat type, see Table 1).

3. Results

3.1. Model

The overall mean daily abundance (ln-transformed; ± SD) was 3.17 ± 0.98, i.e. 23.8 insects (3 min)$^{-1}$ m^{-3}. The meteorological variables included in the best model are shown in Table 2. Temperature was the most powerful meteorological predictor for insect abundance appearing also in the remaining interactions. We found a second-order polynomial relationship between insect number and temperature, indicating a strong increase in insect densities at lower temperatures that levels off at high temperatures (Fig. 1). Precipitations and mean wind speed had a negative effect on insect numbers. However, at low temperatures, the negative effect of wind speed was more distinct than at high temperatures. The daily duration of sunshine had a positive effect on insect numbers, and the interaction revealed that this effect was most pronounced at low temperatures. Thus, at decreased temperatures the flight activity of insects was more sensitive to wind speed or sunshine than in high temperatures (temperature values between 10.5°C and 26°C). In addition to the day-to-day variation, we recorded a seasonal trend in insect abundance in relation to day length, namely, increasing insect abundances up to midsummer followed by decreasing insect numbers. However, the seasonal development of insect abundance was virtually masked by the very large short-term variance due to weather

conditions (Fig. 2). The most parsimonious final model revealed marked differences in insect abundance between habitat types (all pairwise comparisons, Bonferroni corrected: $p < 0.05$, except arable land vs. cereal: $p = 0.068$; Table 3; Table 4, Fig. 1). The maximum abundance (predicted value, ln-transformed; ± SE; holding the other variables at their mean values) occurred at the structural elements (3.69 ± 0.46), followed, in descending order, by cattle pasture (3.48 ± 0.47), grassland (3.13 ± 0.47), cereal (2.91 ± 0.57) and arable land (2.70 ± 0.49). Two interactions remained in the model (Table 3). In open areas (grassland, cereal, arable land), the negative effect of wind speed on flying insect numbers was more pronounced than at structural elements, whereas in cattle pastures, the negative effect of wind was even smaller (Table 4). In contrast, the positive effect of temperature was stronger in grazed and ungrazed grasslands and cereals than in structural elements. Insect abundance over arable land was least affected by temperature. Estimating insect abundances in a defined area in different weather conditions using habitat mapping data showed that the spatial distribution of airborne insects is strongly related to the pattern of habitat structures in agro-ecosystems, most pronounced in adverse weather conditions (Fig. 3).

3.2. Model validation

The linear regression of the observed on the predicted values (year 2001-2003) was highly significant ($F_{1,127} = 188.94$, $P < 0.001$, $n = 129$). Neither the slope nor the intercept of the regression function differed significantly from the expected equality line (slope = 0.983 ± 0.071 SE, $t = 0.185$, $P > 0.05$; intercept = -0.028 ± 0.226 SE, $t = 0.123$, $P > 0.05$). The adjusted R^2 of this regression line was 0.595. Therefore, the shrinkage was 1.4 %, which indicates a high correspondence of the model prediction with the validation data set. The predictions were closely related to the observed values ($r = 0.773$, $P < 0.0001$; $rmse = 0.683$). Regressing the difference between observed and predicted values against the sum of their values resulted in a significant relationship ($F_{1,127} = 18.50$, $P < 0.001$), indicating that the predictions underestimated the observed insect numbers when insect abundance was high (see Fig. 2).

3.3. Regions and years

In 2001, the abundance of flying insects did differ neither between the four regions nor between the different altitudes, when corrected for the local meteorological conditions and habitat types (GLM: regions: $F_{3,234} = 1.63$, $P = 0.183$; altitude within region: $F_{1,234} = 1.86$, $P =$

0.174; corrected model: $F_{12,234} = 34.716$, $P < 0.001$, $R^2 = 0.627$). To test for differences between the five years, we applied the final model to the total data set and included the factor year, which improved the model (number of parameter = 22; $R^2 = 0.612$ vs. number of parameter = 26, $R^2 = 0.620$, ΔAICc = 13.45). However, if we allowed the parameter for day length to vary annually (interaction day length*year), the two models showed no differences (number of parameter = 26, $R^2 = 0.620$, ΔAICc = 0.06), indicating that varying the parameter for day length can account for differences between years (parameter range: 2.260 - 2.585).

4. Discussion

To our knowledge, this is the first study modelling the spatio-temporal variation in the total abundance of flying arthropods near ground level in agri-environments covering both large areas and long periods. The robust and cost effective point-count technique yielded results that were consistent with earlier studies (*meteorological variables:* Taylor, 1963; Pasek, 1988; Pedgley, 1990; Poulsen, 1996; McCarty and Winkler, 1999; Russell, 1999; *habitat types:* Lewis, 1969, 1970; Bowden and Dean, 1977; Peng et al., 1993; Whitaker et al., 2000; Söderström et al., 2001). Beyond that, our model explains over 60 % of the variation in space and time in the abundance of airborne insects considering weather and agricultural variables simultaneously. Therefore it can be applied to predict the density of flying insects and the supply of food for aerial insectivores.

Interactions between weather variables increased their negative effect on insect abundances, i.e. the effects of wind and of the lack of sunshine were most distinct at low temperatures. In such periods of adverse weather conditions, when the abundance of flying insects is low, the remaining patches with flying insects might be most important in the ecology of agri-environments. The highest densities of flying insects were recorded in structural elements, whereas agricultural fields and meadows showed a decreased number of insects in the air, most pronounced in cold and windy weather conditions. Therefore, the abundance patterns were strongly related to the spatial distribution of structural elements in agri-environments. While it has been shown that the species-richness of the above-ground insect fauna is increased at semi-natural structures in agricultural landscapes (Duelli et al., 1999; Thomas and Marshall, 1999; Maudsley, 2000; Atauri and de Lucio, 2001; Duelli and Obrist, 2003; Schweiger et al., 2005), this study confirms that this is also the case with the abundance of flying insects. In order to ecologically improve agricultural landscapes it may be desired to enhance the number and size of patches providing a high abundance of beneficial

insects or representing food sources for aerial insectivore species. We suggest that increasing the structural heterogeneity of agricultural landscapes is a promising way to reach this goal. Almost the same effect might be achieved by increasing the area of cattle pastures. However, the positive effect of pastures on the abundance of flying insects strongly depends on the management regime and the density of cattle (M.U. Grüebler and B. Naef-Daenzer, unpublished data) and therefore should be considered with care (see also Söderström et al., 2001).

The sampling technique did not provide any information about the size and taxa of insects. Therefore, no conclusions on the biomass, the nutritional value or the diversity of airborne insects can be drawn. Furthermore, the results of the present study are based on counts that were conducted just above the vegetation or near structural elements. Hence, the model would require modification if used for higher layers of the air (see Chapman et al., 2002; Reynolds et al., 2005). The point-count method records solely the arthropods in the air. Thus, day-to-day differences in the abundances of airborne insects mainly indicate the varying proportion of flying individuals in the population and population trends should only appear in the seasonal and annual variations. Although the data were log-transformed, the model underestimates peaks in the abundance of insects. This may be due to the formation of swarms in favourable weather conditions. In the presence of swarming insects, the counts may be very high. Since the model is unable to predict the occurrence of swarms out of meteorological and habitat variables, we conclude that the values predicted by the model give a rather conservative estimate for high insect abundances.

The model allows the abundance of airborne insects to be estimated for different periods (e.g. avian breeding periods, culture growing periods) or spatial research units (e.g. individual home-ranges, farm areas, research sites). This provides manifold opportunities for quantitative analyses in ecology, conservation biology or the management of beneficial and pest species. The data required are publicly available and often date back a long way. Climate change and changes in landscape structure due to agricultural policies may affect the temporal and spatial patterns in the abundance of airborne arthropods in the long term. The model therefore offers the opportunity to investigate the effects of past or future changes in meteorological or agricultural variables on insect density, and to estimate ecological and economical consequences of these changes. The results suggest that woody habitats in agricultural landscapes such as shrubs and trees provide not only important nest sites but also crucial food patches to all kind of aerial foragers. Hence, the predicting model can be an important tool to

develop species conservation plans for aerial and perching insectivores in agri-environmental projects.

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Table 1. Sample sizes (observation days, numbers of counts) for the four regions and the five years. The predictive model was built on the basis of a 2-year dataset from the Wauwilermoos area (1999–2000; N = 766 days / 3509 counts; light grey); for model validation a separate 3-year dataset from the Wauwilermoos area was used (2001–2003; N = 129 days / 700 counts; dark grey); different regions and altitudes were compared using data of 2001 (N = 247 days / 1108 counts; bold numbers in italics).

	Wauwilermoos		Vaulruz		Riviera		Pays d'Enhaut		Total	
	Days	Counts	Days	Counts	Days	Counts	Days	Counts	Days	Counts
1999	249	1387	0	0	0	0	0	0	249	1387
2000	517	2122	0	0	0	0	0	0	517	2122
2001	***16***	***32***	***46***	***269***	***68***	***359***	***117***	***448***	247	1108
2002	89	487	0	0	0	0	0	0	89	487
2003	24	181	0	0	0	0	0	0	24	181
Total	895	4209	46	269	68	359	117	448	1126	5285

Table 2. Meteorological model. Model selection of General Linear Models with ln-transformed daily means of insect counts as response variable (N = 766) and the daily meteorological variables temperature (t), sunshine (s), precipitation (p), wind speed (w), day length (d), their square terms and interactions as predictors. Number of parameters (np), the difference in AICc to the best model (ΔAICc) and the adjusted R^2 are shown for the five best models including only meteorological variables (bottom), the five best models including meteorological variables and their square terms (center), the five best models including meteorological variables, their square terms and their interactions (top). The best meteorological model (M: ΔAICc = 0) was used to build the final model including habitat variables (Table 3).

Model	np	ΔAICc	adj R^2
$t+s+p+w+d+t^2+t*s+t*w$	10	0.00	0.460
$t+s+p+w+d+t^2+t*s+t*w+s*w$	11	1.97	0.459
$t+s+p+w+d+t^2+t*s+s*w$	10	4.74	0.457
$t+s+p+w+d+t^2+t*s$	9	5.49	0.455
$t+s+p+w+d+t^2+s^2+t*s$	10	7.37	0.455
$t+s+p+w+d+t^2+s^2$	9	21.50	0.444
$t+s+p+w+d+t^2+s^2+w^2$	10	22.50	0.444
$t+s+p+w+d+t^2+s^2+p^2$	10	23.53	0.443
$t+s+p+w+d+t^2+s^2+p^2+w^2$	11	24.15	0.443
$t+s+p+w+d+t^2$	8	29.11	0.437
$t+s+p+w+d$	7	128.32	0.359
$t+p+w+d$	6	128.98	0.358
$t+s+p+w$	6	134.88	0.352
$t+p+w$	5	135.99	0.351
$t+s+p+d$	6	149.25	0.340

Table 3. Final model. Model selection of the extended meteorological model (M, Table 1) incorporating habitat types (h) and their interaction with the meteorological variables temperature (t), sunshine (s), precipitation (p) and wind speed (w). Number of parameters (np), the difference in AICc to the best model (ΔAICc), the relative support of a particular model compared to the other models (AICc weight) and the adjusted R^2 are shown.

Model	np	ΔAICc	AICc weight	adj R^2
*M+h+h*w+h*t*	22	0.00	0.58	0.609
*M+h+h*w*	18	1.53	0.27	0.606
M+h	14	5.07	0.05	0.602
*M+h+h*w+h*t+h*s*	26	6.05	0.03	0.608
*M+h+h *t*	18	6.39	0.02	0.603
*M+h+h*w+h*s*	22	6.73	0.02	0.605
*M+h+h*w+h*t+h*p*	26	7.50	0.01	0.607
*M+h+h*w+h*p*	22	8.59	0.01	0.604
*M+h+h*s*	18	8.75	0.01	0.602
*M+h+h*w+h*t+h*s+h*p*	30	11.40	0.00	0.607
*M+h+h*p*	18	12.03	0.00	0.600
M	10	233.78	0.00	0.460

Table 4. Parameter estimates (B) and their standard errors (SE) of the final predictive General Linear Model (N = 766) explaining the daily mean insect number in the different habitat types. Meteorological variables were arithmetic means (temperature in °C, wind speed in m/s) and sums (precipitation in 0.1 mm, sunshine in minutes) over 15 daylight hours (from 6.40 h to 21.40 h, Swiss summertime) from the meteorological station Buchs-Suhr (47°23'N 8°05'E). The parameters for structural elements and its interactions are arbitrarily set to zero.

Variables	B	SE
Intercept	-4.36869	1.091
Temperature	0.43791	0.090
Sunshine	0.00457	0.001
Precipitation	-0.00298	0.001
Wind speed	-0.47462	0.129
Day length	3.14035	0.564
Square temperature	-0.00801	0.002
Interaction temperature*sunshine	-0.00022	0.000
Interaction temperature*wind speed	0.02039	0.007
Arable land	0.09047	0.467
Cereal	-1.20271	0.488
Grassland	-0.66366	0.458
Cattle pasture	-0.47678	0.461
Structural elements	0.00000	
Arable land*wind speed	-0.18471	0.062
Cereal*wind speed	-0.04832	0.065
Grassland*wind speed	-0.09175	0.061
Cattle pasture*wind speed	0.03209	0.061
Structural elements*wind speed	0.00000	
Arable land*temperature	-0.03381	0.021
Cereal*temperature	0.02798	0.022
Grassland*temperature	0.01702	0.020
Cattle pasture*temperature	0.01054	0.020
Structural elements*temperature	0.00000	

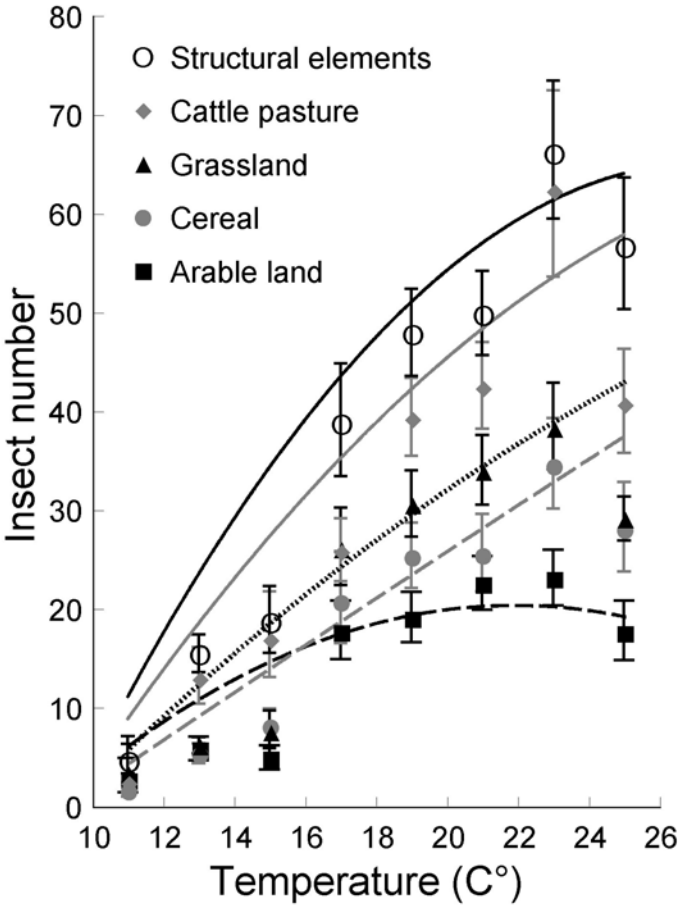

Fig. 1. Mean insect numbers $(3\ min)^{-1}\ m^{-3}$ (back transformed from ln-transformation) in the five habitat types at different daily mean temperatures (data of the predicting model 1999–2000, see Table 1; N = 766 daily means). Lines represent the model predictions, where other meteorological predictors were set to their mean values. Symbols show the original data. Error bars represent standard errors and are asymmetric because of back-transformation. Original data show considerable deviation from model prediction, since they are affected also by meteorological variables other than temperature.

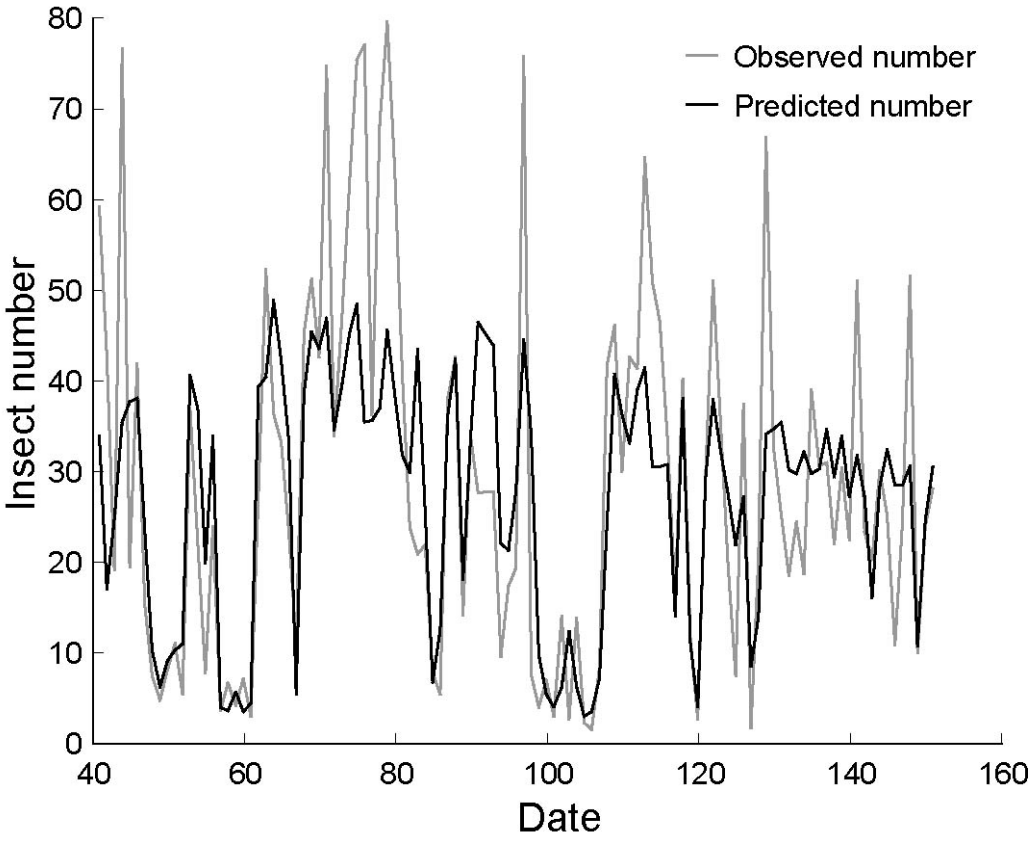

Fig. 2. Observed (grey line) and predicted (black line, back-transformed) daily abundance of airborne insects for the year 2000 as calculated from publicly available meteorological data (habitat parameters set to zero). The values can be interpreted as the daily mean number of insects flying in 1 m^3 air in a 3-minute period. The predictive model underestimates peak values. Date 1 = April 1.

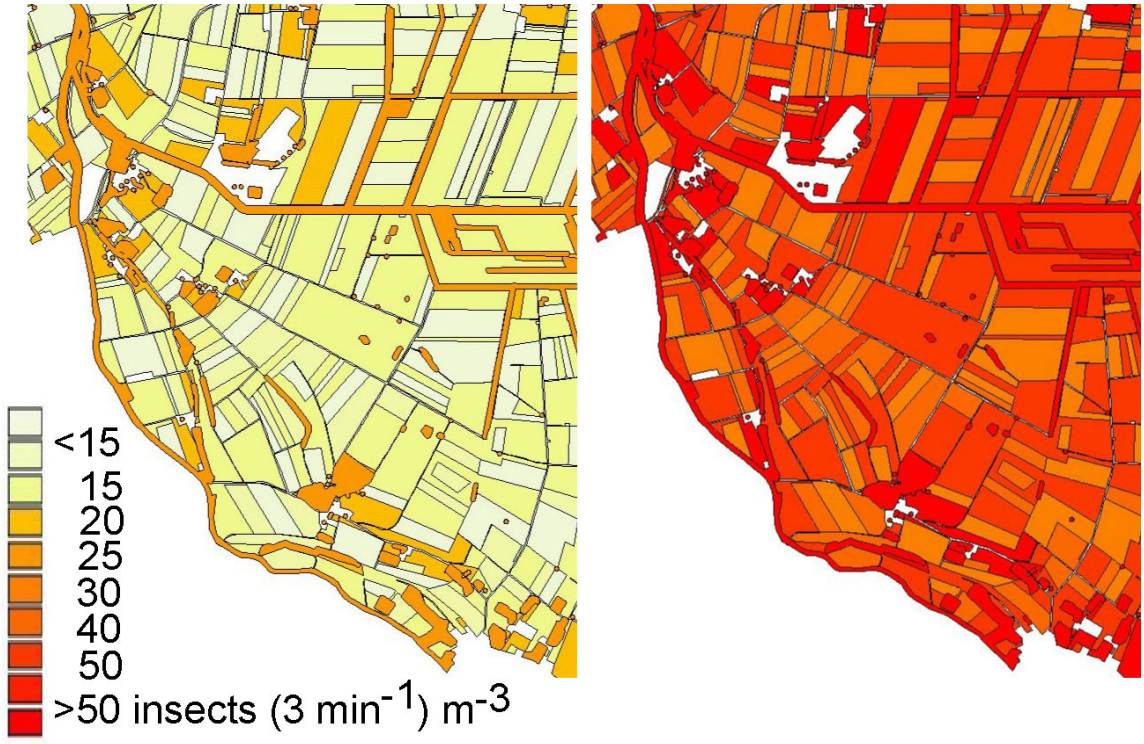

Fig. 3. Predicted spatial distribution and abundance of airborne insects (left) for a rainy day (mean temperature = 15.5°C; 1 h sunshine; amount of precipitation = 10 mm; mean wind speed = 1 ms^{-1}) and (right) for a sunny day (mean temperature = 23°C; 10 h sunshine; no precipitation; mean wind speed = 1 ms^{-1}) in July (relative day length = 0.97).

CHAPTER 2

Estimating local survival from radio-tracking data: effects of transmitter power and sample size

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Summary

1. Cormack-Jolly-Seber (CJS) mark-recapture models estimate local survival on the basis of individual re-encounter histories. Using the barn swallow as an example organism, we analysed the effect of the power of radio-tags on the re-encounter probability, and evaluated the importance of sample size on the performance of CJS-models.

2. Radio-tracking data from 538 radio-tagged and visual records of 22 colour-marked juvenile barn swallows were analysed. We compared the re-encounter rates of four types of radio-tags differing in radiated power. Random sub-samples ranging from 20 to 500 individuals were drawn from the data set to test the effects of sample size on the accuracy and precision of parameter estimates.

3. With all types of radio-tags the re-encounter rates declined with time after leaving the nest, the slope of the decline was inversely related to the radiated power. Hence, the quality of radio-tags had a substantial effect on the probability to recover individuals and in turn, on the temporal resolution and accuracy of survival estimates.

4. The average estimates of local survival (4 groups, 9 encounters) varied little in relation to sub-sample size. However, the variation of individual estimates of local survival and re-encounter probability per group and re-encounter occasion strongly increased with sub-samples of less than 200 individuals. In small sub-samples, the estimates of re-encounter probability deviated frequently from the over-all rate. This in turn resulted in biased estimates of local survival. Accordingly, model selection on the basis of small sub-samples was inconsistent, depending on the composition of particular sub-samples.

5. We conclude that CJS estimates of local survival rates from small samples are robust, and thus yield accurate estimates of local survival rates. If sample size is small, careful modelling of re-encounter probabilities is crucial for the accuracy of survival estimates, e.g. for tests for between-group differences and interactions.

Introduction

Very high frequency (VHF) telemetry is increasingly used to assess key parameters of population dynamics such as differential survival in relation to life history traits (e.g. dispersal and immigration behaviour). This requires radio-tagging of large numbers of individuals to ensure sufficient sample sizes for each cohort of interest, but also that radio-tags remain attached on a long term, often for the animals' entire life. While researchers are aware of the technical difficulty, and of the ethical responsibility, to avoid adverse effects on study animals (review in Kenward 2001), important methodological issues of estimating population parameters from telemetry data remain unclear. Tests of potential tagging effects were frequently added to the main objectives of field studies. Many authors reported no adverse effects (birds: e.g. Brigham 1989; Hill & Talent 1990; Neudorf & Pitcher 1997; Naef-Daenzer *et al.* 2001; Sunde 2005), however, others indicated considerable impact, for example on the allocation of activity time (Hooge 1991), foraging performance (Massey *et al.* 1988, Ackermann *et al.* 2004), and survival rates (Petty *et al.* 2004). By contrast, the impact of the technical reliability of radio-tags on estimates of population parameters has rarely been addressed. Although radio-tracking is invaluable for recovering animals under poor visibility conditions, technical drawbacks such as transmitter failure, and the misinterpretation of signals may introduce additional noise or even bias into the data. For example, "type II errors" in detecting individuals occur if a live individual is incorrectly denoted dead because its transmitter had failed, or vice versa, if a dead individual is denoted alive because the persisting signal of its transmitter was misinterpreted. The technical characteristics (radiated power, life and duty cycle) of radio-tags may also affect the probability of detecting animals (e.g. Nicholls *et al.* 2005). Signals may be missed due to topographic characteristics of the study area, if individuals hide at places that shield radiation (e.g. on the ground or in tree holes), if the animal moves out of the operational range of the transmitter, or in adverse weather conditions (e.g. heavy rain). Consequently, the detection rate of free-ranging radio-tagged animals rarely suffices to determine mortality reliably.

Techniques of mark-recapture analysis allow accounting for the probability of re-encounters and for variance in the recovery probability between cohorts and in relation to the time after tagging and other covariates. These models are based upon individual encounter histories and yield independent estimates of both survival and re-encounter rates (Lebreton *et al.* 1992). Here, we use the barn swallow (*Hirundo rustica* L.) as an example organism to

evaluate the results of CJS mark-recapture models in relation to sample size, transmitter characteristics and behavioural aspects. Specifically, we first test whether the technical performance of radio-tags (particularly radiated power) and behavioural parameters of the study organism (particularly family break-up) affect the re-encounter rates. Second, we evaluate the effects of sample size and selected models upon estimates of survival, which is the target variable of biological importance.

Methods

The data were collected in a study on the post-fledging survival and range use of juvenile barn swallows that was carried out in 2000 (pilot study) and 2002 - 2004 (full project) in the Wauwilermoos area, an intensively cultivated plain of c.20 km^2 near Lucerne, Switzerland (47°10' N / 8° 02' E). Tracking data from 132 first and second broods at 60 farms were included.

RADIO-TAGGING

We caught the fledglings at their nest during the night of nestling day 19 or 20. In 2000 (pilot study) the chicks were radio-tagged with Holohil LB2 transmitters (0.7 g, Holohil Inc.). In 2002-2004 we used radio-tags of own construction (Naef-Daenzer 1993; Naef-Daenzer *et al.* 2005). These differed from the LB2 transmitters in an extended life of 30 d (2002) to 55 d (2004). Due to technical improvements the radiated power of these tags increased considerably from 2002 to 2004 (Tab. 1, Naef-Daenzer *et al.* 2005). All radio-tags (including battery and harness) had a mass of 650 to 750 mg, which represents 3.8 – 4.4 % of the minimum fledgling mass (17 g).

The transmitters (n = 538) were attached using a Rappole-type harness made from 0.5 mm elastic cord (Rappole & Tipton 1990; Naef-Daenzer 2007). The juveniles were also individually colour-marked on the light plumage of the belly to allow identification after loss or failure of transmitters. A combination of two colours out of four (green, blue, red, none) was applied using waterproof pencil (Edding 3000®). These patterns occurred repeatedly among families. Additionally, a family-specific mark was applied. To prevent premature departure the nest cups were closed using a flexible sheet of black plastic. The marked chicks were set back into the nest in complete darkness. We then waited 5-10 min until the birds had relaxed, and removed the cover.

Earlier studies did not find adverse effects of radio-tagging on small birds of c. 20 g (barn swallow: Brigham 1989, great tit (*Parus major*) and coal tit (*P. ater*) fledglings: Naef-Daenzer *et al.* 2001). Therefore, we included only a small control group of untagged birds. The treatment of these birds (n = 22) was identical to the above procedure except that no transmitter was attached.

ENCOUNTER HISTORIES

The families and independent juveniles were located twice per day. The observation sessions lasted one hour and included the location and visual identification of the birds, and the collection of behavioural data. Emphasis was given to avoiding "type II errors" in encounter histories by frequent visual observation of the tagged birds. Before family break-up, all individuals could be checked visually as long as one transmitter per party was working. Missing birds were searched within an area of approximately 100 km^2 using fixed antenna stations on vantage points and by using vehicles equipped with an omni-directional antenna. Additionally, flocks of swallows in the study area and groups of birds roosting inside buildings were searched for individuals with colour-marks. We never recorded radio-tagged birds leaving the area within the first 3 weeks post-fledging, which indicates, that the birds did not emigrate from the area up to this age. All telemetry and visual observations were used to build daily encounter histories for the analysis of survival and re-encounter rates (fledging day 1 = first re-encounter).

STATISTICAL ANALYSES

We used Cormack-Jolly-Seber (CJS) mark-recapture models (Lebreton *et al.* 1992; Anderson & Burnham 1994) in the software package MARK (White & Burnham 1999). The individual encounter histories were used to model probabilities of survival (Φ) and re-encounters (p). We built encounter histories for 9 time intervals of 1-10 days (post-fledging days 1, 2, 3-6, 7-10, 11-14, 15-18, 19-22, 23-29, 30-39). A goodness-of-fit test was performed on the basis of a highly parameterised model, including variation in survival in relation to age and differences between first and second broods, and variation of the re-encounter rate in relation to age and transmitter type, but excluding interactions ($\Phi_{(\text{brood}\cdot\text{age})} p_{(\text{type}\cdot\text{age})}$). We performed a parametric bootstrap with n = 100 replicates. The observed deviance (dev. = 3025.14) did not differ significantly from the simulated deviances (mean dev. = 2950.38 ± 10.04 s.e., p = 0.22), indicating that our set of models adequately fitted the data. The overdispersion factor ĉ was

1.192. Slight overdispersion was likely to occur, since cohorts were not equal in size, and fledglings of the same family were treated as independent (see Anderson & Burnham 1994).

SUB-SAMPLING

To simulate the effects of sample size on the estimates of survival (Φ) and re-encounter rate (p) we drew a total of 50 sub-samples of varying size from the full sample of 538 radio-tagged individuals. Random sub-samples were drawn with replacement and the exact sample size was determined using the random number generator in the software Excel (Microsoft Inc.). To further evaluate the performance of model selection we split the full sample into 10 random sub-samples of 50 individuals each, i.e. without replacement. For all sub-samples the 16 pre-defined models implemented in MARK were compared. The overdispersion factor ĉ of 1.192 was also applied to these models.

Results

TRANSMITTER EFFECTS ON RE-ENCOUNTER RATES

The most parsimonious model on the basis of the full sample included a relationship between survival rate and time after fledging but no effect of the type of marking (radio-tag/colour) on survival (Tab. 2). Including a survival effect of radio-tagging resulted in a slight increase of the QAICc. In both models discerning colour-marked and radio-tagged birds (ranks 2 and 3, Tab. 2) the differences in survival estimates for colour-marked and radio-tagged individuals were small. The average daily survival during the first 15days after fledging was 0.948 in radio-tagged and 0.944 in colour-marked birds, respectively. If at all significant, the estimates would suggest higher survival of radio-tagged individuals. This accords with earlier evidence from larger samples that radio-tags had no measurable impact on juvenile survival during the first 15 days post-fledging.

The top ranked model also showed a strong effect of both time after fledging and type of transmitter on the re-encounter probabilities. Figure 1 illustrates that the effect of the transmitter type on the reencounter rates was substantial and apparently related to the radiated power of the tags. Over all age classes the re-encounter rate of colour marked individuals was lowest. In the first days after fledging, the probability to recover colour-marked birds was about 0.8. However, this rate declined quickly with age and was c. 0.3 when the families broke up. After family break-up, recoveries of colour marked individuals occurred only occasionally. Compared to this figure, all radio-transmitters markedly improved the re-encounter rates, and

individuals could be recovered reliably beyond family break-up. In the first 5 days from fledging the re-encounter rate of radio-tagged individuals was close to 1.0 with all types of radios. In this period the range used by families was small but the chicks frequently hid in trees. Hence, transmitter power was not critical for re-observing the birds. However, from post-fledging day 6, the families, and later on the independent juveniles, moved quickly over distances of up to 15 km. Accordingly, the re-encounter rate decreased in relation to both age and transmitter power. The daily re-encounter rate after one month was 0.28 ± 0.07 s.e. in 2002, 0.39 ± 0.07 in 2003 and 0.75 ± 0.08 in 2004 (Fig. 1).

EFFECTS OF SAMPLE SIZE

Estimates of local survival and re-encounter probability

The respective most parsimonious models for the 50 sub-samples and the full sample varied relatively little in the estimates for local survival and re-encounter probability. Similar to the full-sample model, sub-samples revealed relatively high daily survival rates in the first days after fledging (re-encounters 1-3) which declined to a minimum around day 15 post-fledging (re-encounters 6, 7) and then recovered again for fledglings older than 16 days post-fledging (Fig. 2). However, according to the prediction from statistical theory, the variation of the estimates of both survival and re-encounter rate increased inversely to sub-sample size (Fig. 2, 3a). The individual estimates deviated considerably from the reference value from the full sample when sub-sample size was small. In addition to these 'trumpet-shaped' relationships, we found a marked negative correlation between the estimate for the re-encounter rate and that of local survival (Fig. 3b). Compared to the full sample, under-estimation of p resulted in over-estimation of Φ and vice versa. This bias was particularly large with samples of less than 100 individuals (light grey dots in Fig. 3b). These results indicate that the precision of the estimates strongly improved with sample size and reached an asymptote only at a sub-sample size of c. 200 individuals.

In accordance, the model selection was highly inconsistent with small sub-samples. For example, figure 4 gives the ranking of 6 arbitrarily chosen models (out of the 16 pre-defined models) in relation to sub-sample size for all 51 runs. Since the AICc favours simple models if the sample is small, the finally favoured model $\Phi(t)\ p(g \cdot t)$ was ranked very low (ranks 12-15) when sub-sample size was small. The ranking of this model increased quickly and from sub-sample size 260 this model was invariably favoured. However, the ranks of the model in every single sub-sample (dots in fig. 4) varied extremely, which indicates a strong effect of the

particular sub-samples on model selection. Similarly, the ranking of the other models varied greatly with sub-sample sizes below c. 200. Stable rankings were reached at sub-sample sizes of c. 200 for the simplest model (Φ(.) p(.)) to 380 for the most complex model (Φ(g·t) p(g·t)). The final ranks were reached at a large proportion of the full sample, thus it is impossible to exclude that the effect was caused by the increasing similarity of the respective sub-samples in relation to the proportion of the full sample that was drawn.

Comparing the favoured models for the 10 entirely different sub-samples of 50 individuals each further emphasised that variation in the encounter histories within the sub-samples had a strong effect on model selection. Out of the 8 'simple' models (i.e. those without group·encounter interactions) 5 were favoured at least once. The respective QAICc weights ranged from 0.549 to 0.921, and in 8 of the 10 cases the ΔQAICc to rank 2 exceeded 2.0. With regard to local survival the conclusions drawn upon one particular sub-sample would therefore differ considerably: 1) local survival is constant over groups and re-encounters (Φ(.), 5 models, 2) local survival differs amongst transmitter types (Φ(g), 3 models), and 3) local survival differs amongst encounters (Φ(t), 2 models). We conclude from this that model selection on the basis of a sample of 50 individuals was sensitive to the particular composition of the samples, and thus that a sub-sample size of 50 did not represent the statistical population.

Discussion

The analyses and simulations revealed that CJS-models yielded consistent estimates of local survival even with small samples, compared to the results from the full sample of 538 radio-tagged individuals. Models using small sub-samples also showed the apparent depression in survival rates following family break-up. The main conclusion from these results is that estimates of local survival from small samples are robust in respect of the general patterns in local survival, which is a key parameter of population dynamics.

By contrast, the variation in parameter estimates from small sub-samples was large, and comparing the modelling results for 10 entirely different sub-samples of 50 birds each suggested that model selection was highly sensitive to the particular composition of small sub-samples. Thus, point estimates for groups and/or encounters obtained from small samples may deviate substantially from the statistical population. This indicates that inference upon a specific model, and on related biological mechanisms should be drawn carefully and should be supported by additional evidence if samples are small (Burnham & Anderson 1992). Even if

the difference in QAICc to lower ranked models was large, alternative models were difficult to discern due to the uncertainty in estimates for both parameters. A probable cause for the inconsistent results of model selection is that all cohorts gradually decline in numbers due to mortality. If the initial sample is small, the basis for estimates at later re-encounters declines to a very few individuals, hence to have missed or encountered one individual at a particular occasion has a strong effect on the modelling results (Rexstad *et al.* 1992, Burnham & Anderson 1992).

Our results underline the importance of adequate modelling of the re-encounter probabilities in order to maximise the accuracy of survival estimates, in particular for small sample sizes. Bias in the estimates of the re-encounter probability had a substantial effect on survival estimates (Fig. 3b, Zabel *et al.* 2005). In our examples, the estimates for the average daily local survival in the first three weeks post-fledging ranged from 0.941 to 0.982. Although numerically small, this variation would result in large differences in estimates of life expectancy or of the proportion of juveniles surviving the first three months.

Compared to colour-marked birds, the re-encounter rate of radio-tagged birds was much higher throughout the post-fledging period, and radio-tagged individuals were reliably recovered beyond 50 days from fledging. Particularly the final transmitter version used in 2004 allowed the birds to be recovered at an excellent rate. Our analyses indicate that the power and the technical performance of radio-tags are important issues in maximising data quality, and in turn, model accuracy. Furthermore, the radiated power of radio tags is of practical importance since strong reliable tags greatly reduce the search effort per recovery. This also improves the temporal resolution of the data and survival models, which is crucial for studies aiming at quantifying the temporal and between-cohort variation in local survival.

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Table 1. Sample sizes and technical specifications for the different types of markings used in the study

Year	Mark Type	Radiated power	Tag life, d	N	Comment
2000	Colour mark			14	
2002				8	
2000	Holohil LB2	35 µW (-15.2 dBm)	13-21	46	www.holohil.com
2002	Own, one stage	13 µW (-18.5 dBm)	30-35	203	ZA10 ZnO2 cells
2003	Own, one stage	23 µW (-16.3 dBm)	30-35	203	396 AgO cells, Harness on transmitter
2004	Own, one stage matched antenna	48 µW (-13.1 dBm)	50-60	86	396 AgO cells, Harness on cell

Table 2. Model selection for post-fledging survival probabilities of barn swallows. For each model, the value of deviance, number of parameter (np) , the modified Akaike's Information Criterion (QAICc) and the QAICc-deviation to the best model (ΔQAICc) are given. For all models an overdispersion factor ĉ = 1.192 was used. Model notation: Φ: survival probability, p: re-encounter probability, +: additive effect; ·: interaction; *tag*: radio-tagged/colour marked; *type:* category of radiated power.

Model	QAICc	ΔQAICc	np	Deviance
$\Phi_{(age)}\ p_{(type \cdot age)}$	5904.93	0.00	47	5810.22
$\Phi_{(tag+age)}\ p_{(type \cdot age)}$	5905.34	0.42	48	5808.61
$\Phi_{(tag \cdot age)}\ p_{(type \cdot age)}$	5907.57	2.65	52	5802.71
$\Phi_{(age)}\ p_{(type+(tag \cdot age))}$	5930.86	25.94	26	5878.64
$\Phi_{(age)}\ p_{(type+age)}$	5935.14	30.21	20	5895.01
$\Phi_{(age)}\ p_{(tag \cdot age)}$	6094.60	189.67	23	6048.43
$\Phi_{(age)}\ p_{(tag+age)}$	6094.69	189.77	16	6062.61
$\Phi_{(age)}\ p_{(age)}$	6180.66	275.73	15	6150.58
$\Phi_{(age)}\ p_{(.)}$	6700.32	795.39	9	6682.29

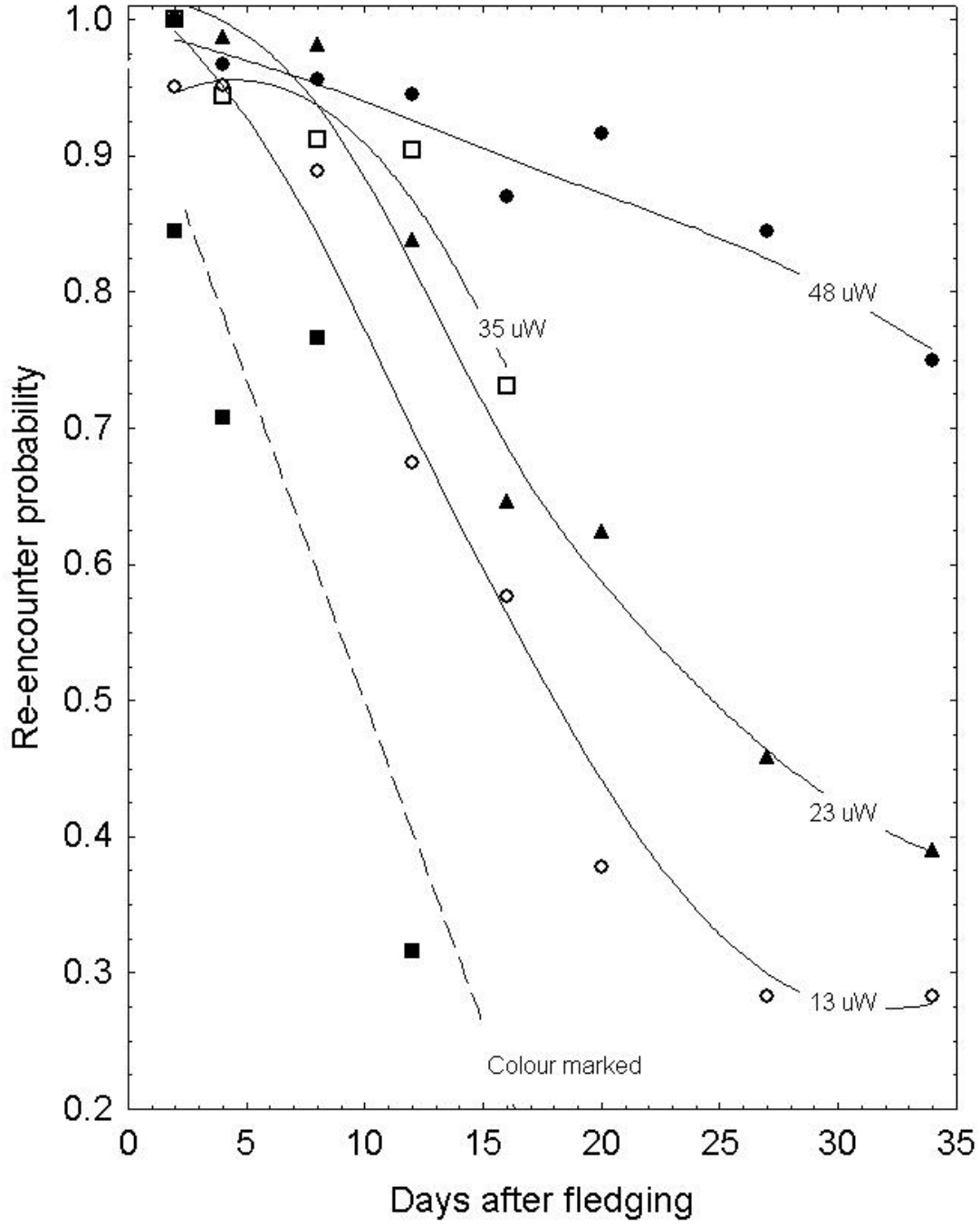

Fig. 1. The re-encounter probabilities (*p*)in relation to time after fledging of colour-marked and radio-tagged juvenile barn swallows as calculated using the full sample of 560 marked birds. Transmitter specifications and cohort sizes are given in Table 1. Colour-marked birds were not recovered regularly after family break-up, i.e. 12-15 days after fledging. The life of 35 µW tags was below 20 d. Trend lines were fitted by distance-weighted least squares, except for colour marks (linear trend).

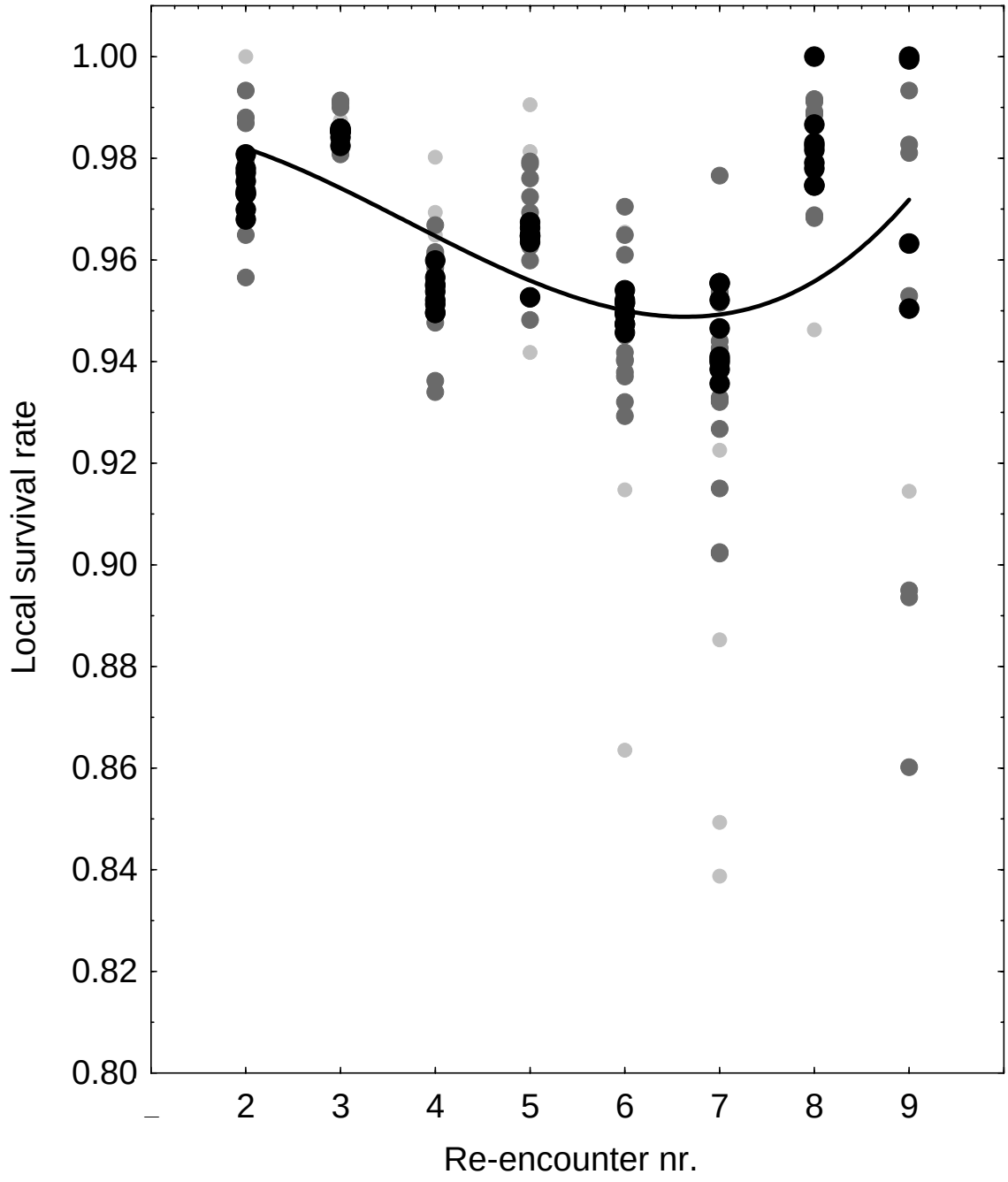

Fig. 2. Estimates of daily local survival (Φ) from all sub-sample models for re-encounters 2-9 and 3 categories of sub-sample size. In general the models gave similar results and revealed a depression in local survival following the break-up of families (i.e. around day 15 from fledging). Dot size and colour indicate sample size categories. Small, light grey: n < 100; medium, grey: n = 101 to 300, large, black: n > 300. The line gives the polynomial regression on all estimates ($y = 0.98 + 0.0057x - 0.0041x^2 + 0.0004x^3$).

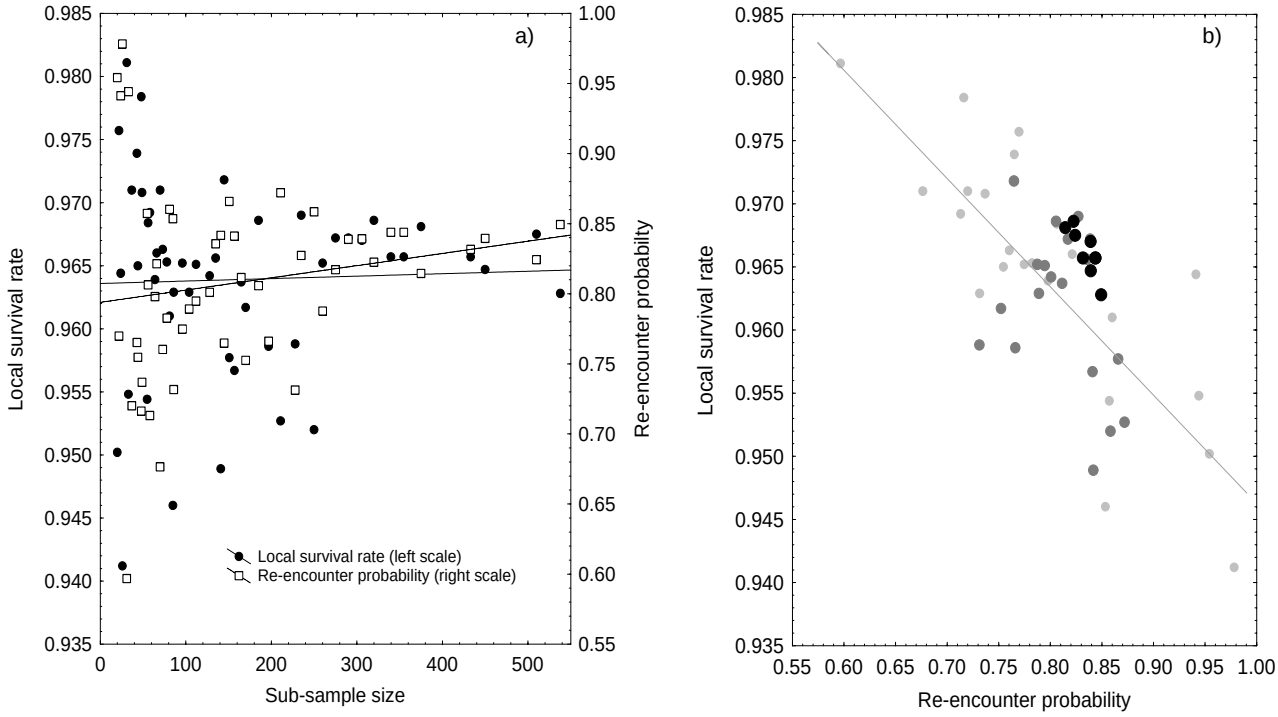

Fig. 3. a) Average estimates for local survival (Φ) and re-encounter rate (p) over all re-encounters in relation to sub-sample size. In both parameters the variation of estimates strongly increased inversely to sub-sample size. b) Estimates of local survival in relation to re-encounter probability. Small sub-samples were likely to give biased estimates of the re-encounter rate and in turn, local survival. Dot size and colour indicate sample size categories as in fig.2. The line gives the regression for samples of < 100 individuals (y = 1.03-0.085x).

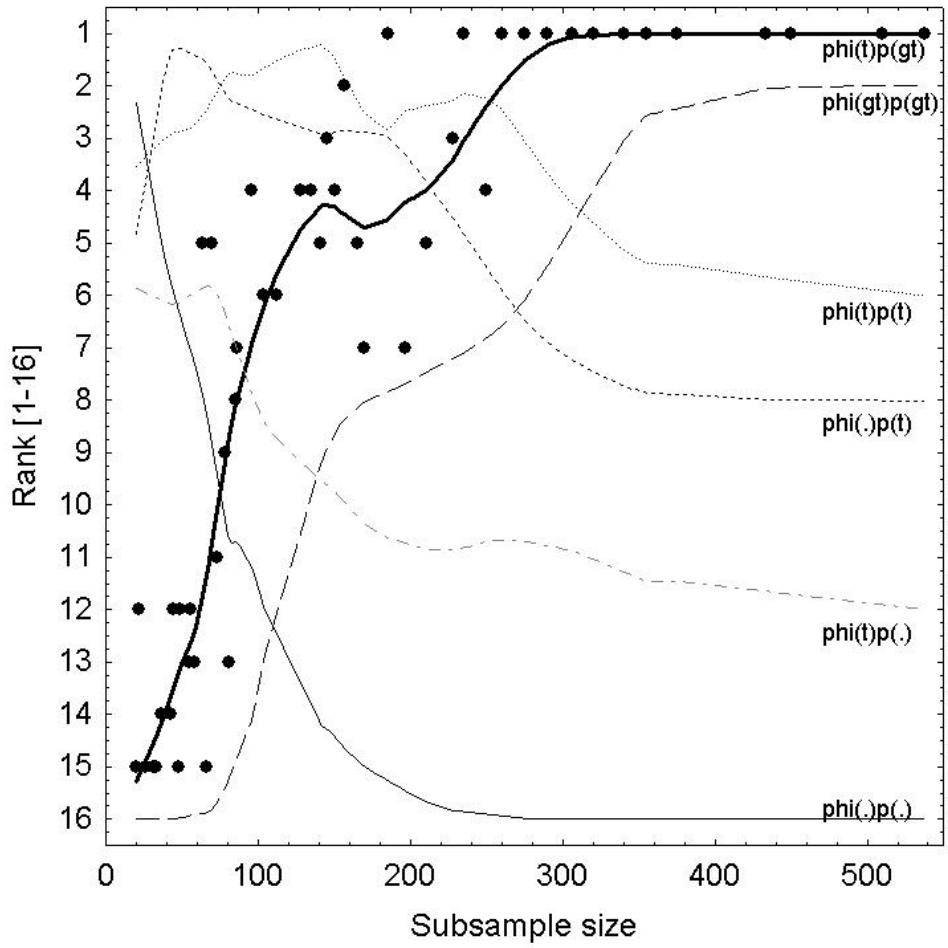

Fig 4. The ranking of 6 arbitrarily selected models (out of the 16 pre-defined models in MARK) to illustrate the changes in model selection results in relation to sub-sample size. Lines represent distance weighted least-squares fits on the ranks obtained for each of the 51 runs. For the top-ranked model, dots give also the individual ranks for each sample.

CHAPTER 3

Fitness consequences of timing of reproduction and post-fledging care of second broods in the barn swallow (*Hirundo rustica*)

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Summary

1. In double-brooded species, the fitness consequences of timing expressed in second broods are expected to affect the temporal characteristics of the whole annual breeding system. A major problem in quantifying the fitness-relevance of the timing is that individual differences between pairs may cause the seasonal trend, if the timing is also related to the rearing competence of the parents.

2. The differentials in juvenile survival due to parental pre-fledging timing decisions often only appear after the fledging of the chicks. As care continues in the post-fledging period, parental decisions continue to influence juvenile survival.

3. We tested the effects of timing and parental competence on the post-fledging survival of second brood juvenile barn swallows (*Hirundo rustica* L.) by swapping earlier and later hatching clutches and radio-tracking the juvenile subjects. The mark-recapture models included estimates of food supply and the duration of post-fledging care to facilitate consideration of the role of seasonal declining ecological conditions in post-fledging effects.

4. There was an annually varying negative seasonal trend in offspring survival, which was associated with environmental conditions, i.e. with declining food availability. Directional selection for early breeding occurred in the two years with scarce autumnal food supply. Furthermore, we found strong selection for long post-fledging parental care. However, date did not affect duration of care. Neither did longer care compensate for the seasonal decline of juvenile survival.

5. The reproductive output was determined by two parental timing decisions: the timing of breeding and the timing of family break-up. Differential fledgling survival of second brood chicks in relation to these decisions is an important part of the selective mechanisms shaping the reproductive system of barn swallows.

Introduction

The timing of reproduction is one of the most prominent breeding decisions and a major determinant of reproductive success in birds (overview in Clutton-Brock 1988; e.g. Daan, Dijkstra & Tinbergen 1990; Magrath 1991). Generally, the reproductive performance decreases with season either due to declining clutch size (e.g. Winkler & Allen 1996), decreasing nestling and post-fledging survival (e.g. Wiggins, Pärt & Gustafsson 1994; Naef-Daenzer, Widmer & Nuber 2001a), or recruitment rates (Hochachka & Smith 1991; Brinkhof, Cavé & Perdeck 1997; Svensson 1997). Hypotheses from life history theory postulate two main underlying mechanisms. First, the *parent quality hypothesis* proposes that the high reproductive output of early breeders is explained by a negative relationship between the start of reproduction and the parents' physical condition and physiological and behavioural competence, i.e. the strongest birds breed earliest (Parsons 1975; Hatchwell 1991; Brinkhof *et al.* 1993). Second, the *date hypothesis* proposes that the seasonal decline in reproductive performance is caused by seasonal variation in crucial ecological factors (e.g. food, predation) or by physiological processes (e.g. moult, preparation for migration), irrespective of parental competence (Hatchwell 1991; Brinkhof *et al.* 1993; Moreno 1998). The two mechanisms are not mutually exclusive and both, parental competence and seasonal effects, may act during different phases of the life cycle and with differing intensity (review in Nilsson 1999). In many species, the resulting differentials in juvenile survival are most likely to occur only after fledging. This poses many observational problems. Consequently, the relationship between parental breeding decisions and post-fledging fitness costs or benefits have rarely been investigated (Anders & Marshall 2005).

During the first weeks after fledging, young birds learn crucial life skills (Davies 1976; Marchetti & Price 1989; Wheelwright & Templeton 2003; Yoda, Kohno & Naito 2004), and the risk of death by predation is very high (Anders *et al.* 1997; Naef-Daenzer *et al.* 2001a; Kershner, Walk & Warner 2004; Davies & Restani 2006). Parents still provide supplementary food and invest efforts in brood defence during this period (e.g. Leedman & Magrath 2003; Pavel 2006). The duration of this post-fledging parental investment is likely to affect juvenile survival (Russell 2000; Cam, Monnat & Hines 2003) and should be considered in studies on differential post-fledging survival. In particular, post-fledging time investment of parents, if seasonally declining, may cause a seasonal decline in reproductive output as proposed by the *parent quality hypothesis*. Alternatively, longer post-fledging parental care might compensate

for reduced juvenile survival due to declining environmental conditions or due to less competent parenting (De Neve *et al.* 2004).

In double-brooded species, the reproductive value of the second clutch contributes much to the total annual reproductive output (Ogden & Stutchbury 1996; Visser *et al.* 2003; Nagy & Holmes 2005). However, the timing of the two broods and the allocation of efforts amongst the broods are interdependent, hence timing-related fitness consequences expressed in the second brood will affect the temporal patterns of the whole reproductive system.

Here, we demonstrate that in the double-brooded barn swallow (*Hirundo rustica* L.), both the timing of second broods and the duration of post-fledging care cause strong differentials in the survival rate during the first three weeks after leaving the nest. First, we present an experiment to test if the parental rearing competence or the timing of breeding determines the post-fledging survival of second brood chicks. Second, we quantify the year-to-year variation in the impact of timing effects in terms of selection differentials. Third, we examine the correlation between the duration of post-fledging parental care and juvenile survival: a positive relationship might suggest a causal link or a compensatory reaction to seasonal effects. The resulting models help understand the fitness consequences of parental reproductive decisions and lend insight into the ecological and evolutionary mechanisms that shape temporal reproductive characteristics through differential survival.

Materials and methods

The study was carried out from July to September in 2000 and 2002 – 2004 in the Wauwilermoos, an agricultural area of c.20 km^2 near Lucerne, Switzerland (47°10’ N, 8° 02’ E). The nests of the barn swallow (*Hirundo rustica* L.), a double-brooded socially monogamous long distant migrating passerine, were visited weekly at 60 farms. We determined the laying date by assuming that females lay one egg per day. Towards the end of the incubation period, nests were inspected daily to record the exact hatching date (date, when the first egg hatched = day 1 of the nestling period). The earliest second brood fledged on 14 July, the latest on 18 September.

FOOD SUPPLY

The density of flying insects was recorded using a modified method according to Flaspohler (1998). A white board (0.7 m x 0.5 m) was mounted about 0.1 m above the field vegetation level. We counted the insects passing in front of the board during a period of 3 minutes using

binoculars (10 x 42) at 10 m distance. Insects with a body length of more than 1.5 mm were visible if they moved into the field of focus, i.e. 4.2 m from the white board. Thus, we counted insects passing a volume of approx. 1 m^3 air. By correlating daily mean counts with meteorological variables (temperature, wind, precipitation and sunshine) we built a model that allowed the daily food supply to be estimated from meteorological data. Validating the model using an independent data set (collected in the study area) proved that the daily food supply can be accurately estimated using meteorological data that are publicly available (Grüebler & Naef-Daenzer 2007). Here, we use predicted daily insect densities to account for variation in food supply. For each year, we calculated (1) a mean daily food supply (in number of insects $(3\ min)^{-1}\ m^{-3}$) from 15 July to 30 September, and (2) the slope of the decline in daily food supply in the same period (Table 1). Years with a steep decline (slope < -0.3) were categorized as years with scarce autumnal food supply, whereas a moderate decline (slope > -0.3) suggested a favourable autumnal food supply.

EXPERIMENTAL PROTOCOL

The timing of hatching of second clutches was manipulated by swapping two complete clutches of similar size (± 1 egg) but different laying dates. Thus, early-laying parents received a clutch expected to hatch later (delayed broods), whereas the late-laying pair received a clutch expected to hatch earlier (advanced broods). The manipulation resulted in differences in the fledging date of 3 to 10 days between pairs with exchanged clutches. 48 second clutches were exchanged (2002: 28 clutches; 2003: 20 clutches), creating 24 advanced and 24 delayed broods. Another 25 randomly selected second broods of the years 2000 and 2002 – 2004 were used as un-manipulated control broods.

RADIO-TAGGING

The broods fledged at an age of 20 to 26 days. We caught the nestlings in their nests during the night of day19 or 20. All chicks were radio-tagged with a miniature transmitter of own construction (Naef-Daenzer 1993; Naef-Daenzer *et al.* 2005). The radio-tags (including battery and harness) weighed 650 to 750 mg, which is 3.8 – 4.4 % of the minimum fledgling mass (17 g). The aerial consisted of 10 cm of 0.15 mm multistrand steel. The tags operated for 3 to 5 weeks, and had a range of 2 to 5 km. Due to technical improvements tag life and range increased during the study. The transmitters were attached using a Rappole-type harness made from 0.5 mm elastic cord (Rappole & Tipton 1990). All juveniles were individually colour-

marked on the light plumage of the belly to allow identification after eventual loss or failure of transmitters. A combination of two colours out of four (green, blue, red, none) was applied using waterproof pencil (Edding 3000®). These patterns occurred repeatedly among families. Additionally, every fledgling was coloured with a family-specific mark. To prevent premature departure the nest cups were closed using a flexible sheet of plastic. The marked chicks were set back into the nest in complete darkness. We waited 5–10 min until the birds had relaxed, and then removed the cover. A pilot study in 2000 did not reveal any quantitative or qualitative differences in behaviour, flight activity, manoeuvrability, and survival between radio-tagged juveniles and a control group of colour-marked but untagged fledglings (own unpublished data). For a test of possible adverse effects of radio-tagging juvenile birds see also (Naef-Daenzer, Widmer & Nuber 2001b).

Out of the 48 experimental clutches, 5 clutches (4 delayed and 1 advanced) did not hatch and 2 broods (1 delayed and 1 advanced) did not survive to fledging. Out of the remaining 41 experimental broods, 4 delayed broods were missing at the night of day 20 probably due to early fledging and therefore were not radio-tagged, leaving 37 experimental broods (22 advanced broods, 89 fledglings; 15 delayed broods, 58 fledglings). Further, 96 fledglings of 25 un-manipulated control broods were included into the analysis. In total, we obtained survival data of 243 fledglings.

ENCOUNTER HISTORIES AND PARENTAL CARE

The families and independent juveniles were located twice per day. The observation sessions lasted one hour and included the location and visual identification of the birds, and the collection of data on feeding behaviour of parents. Based on this information, the duration of post-fledging parental care (DPC) was denoted the period from fledging to the last observed feeding (in 1 d increments). Emphasis was given to avoiding type II errors in encounter histories due to telemetry (e.g. dead bird with working transmitter denoted alive, or living bird with broken transmitter denoted dead) by frequent visual observation of the tagged birds. Before family break-up, all individuals could be checked visually as long as one transmitter per party was working. Missing birds were searched within an area of approximately 100 km^2 using fixed antenna stations on vantage points and by using vehicles equipped with an omni-directional antenna. Additionally, flocks of swallows in the study area were searched for birds with colour-marks. We never recorded radio-tagged birds leaving the area within the first 3 weeks post-fledging, which indicates, that the birds did not emigrate from the area up to this

age. All telemetry and visual observations were used to build daily encounter histories for the analysis of survival and reencounter rates (first reencounter = fledging day).

STATISTICAL ANALYSES

For survival analyses we used Cormack-Jolly-Seber (CJS) mark-recapture models (Lebreton *et al.* 1992; Anderson & Burnham 1994) in the software package MARK (White & Burnham 1999). Individual encounter histories were used to model probabilities of survival (*Φ)* and reencounter (*p*) separately. To reduce the number of parameters 12 age classes were defined (post-fledging days 1–2; 3–4; 5–6; 7–8; 9–10; 11–12; 13–14; 15–16; 17–18; 19–21; 22–28; 29–38) The goodness-of-fit of the final model to the data was assessed by bootstrapping excluding individual covariates ($\Phi_{(year+age)} p_{(year+age)}$). The probability of a deviance equal or larger than the observed value was 0.152. Thus, the CJS modelling approach was appropriate. The overdispersion factor ĉ was 1.277 and was used for all present models. Slight overdispersion was likely to occur, since groups were not equal in size, and fledglings of the same family were treated independently (see Anderson & Burnham 1994).

First, we modelled the reencounter probabilities while keeping the survival rate constant (results in Table 2). Subsequently, we analysed the post-fledging survival using the best reencounter model (results in Table 3). The effects of fledging date (covariate) and treatment (factor with three states: advanced, delayed, control) on juvenile survival were tested under the two hypotheses, controlling for possible environmental and parental effects of the post-fledging period i.e. the mean food supply of year (covariate) and the duration of post-fledging parental care (DPC, covariate). DPC was assumed to be an important variable in both modelling reencounter and survival probabilities. In 7 families all the fledglings died before parental care was terminated. In these families, DPC was set to the mean value, calculated among all the other families in the data set (13.15 ± 3.05 days, N = 55); hence theses families did not contribute to the variation. Between-year variation was tested for years with favourable and scarce autumnal food supply (Table 1). Furthermore, we included the interactions between fledging date and year and between treatment and year. For models with covariates we used a logit link function. Model selection was based on the corrected Akaike Information Criterion (QAICc; Burnham & Anderson 1998; White & Burnham 1999).

Results

REENCOUNTER PROBABILITY

The best reencounter model included the effects of chick age, technical changes (between years), DPC and date on reencounter probabilities (Table 2). First, the observation probability declined in relation to age due to the increasing mobility of the families and newly independent juveniles. Second, the reencounter rates differed between years because the range and battery life of the radio-tags improved during the study. Third, the most parsimonious model also supported a positive effect of DPC on the reencounter probability. This was because independent juveniles covered larger day-to-day distances than did intact families. Fourth, the reencounter rates increased towards the end of the season probably due to the formation of large flocks in which juveniles were easily detected.

EFFECTS OF DATE AND PARENTAL QUALITY

The six top-ranked models included a strong decline of survival rates in relation to fledging date (Table 3: model 1 – 6). The most parsimonious model yielded survival estimates that differed according to the food supply of the year and included year specific date effects (Table 3). In years with a high average food supply the post-fledging survival was increased (Beta = 0.49 ± 0.13 SE; Fig. 1a). Years with favourable autumnal food condition (2000, 2003) showed a slight seasonal decline in post-fledging survival (Beta = -0.12 ± 0.12 SE; Fig. 1a), whereas in years with scarce autumnal food supply (2002, 2004) survival declined steeply (Beta = -0.51 ± 0.13 SE; Fig. 1a). The model fit was not improved by including the experimental treatment (Table 3: models 1 & 2 vs. models 3 & 4), indicating that the data support no difference between the experimental groups. Fig. 2 shows the seasonal decline for the three experimental groups as suggested in model 3, which is the best model including the experimental groups (Table 3). In the *parental quality hypothesis* delayed broods are expected to have higher survival probabilities than control or advanced broods. In contrast, delayed broods showed slightly lower survival probabilities. We conclude from this, that the fledging date rather than variation in parental quality was the main determinant of the decline in post-fledging survival in second brood chicks. The marked difference in the slope of the decline in survival rates between years with good and poor food supply is further support for the *date hypothesis* and suggests that the declining food resources are the main cause for the seasonal trend.

EFFECT OF PARENTAL CARE

In addition to the date effect and the between-year variation in post-fledging survival, the most parsimonious model also included a positive relationship between DPC and chick survival (Table 3; best model: Beta = 0.20 ± 0.08 SE;). The average DPC for second broods was 13.15 ± 3.05 days (range 9 – 24 d, n = 55). The model suggests that chicks receiving longer parental care survived substantially better than those receiving care for only a short period after leaving the nest (Fig. 1b), the effect being additive to the seasonal trend in post-fledging survival. We found no linear relationship between fledging date and DPC (r = -0.093, $P = 0.497$, n = 55). Correcting for annual differences in the mean DPC still did not reveal a correlation. Nor did we find a significant difference of DPC amongst treatments ($F_{5,49} = 0.968$, $P = 0.447$; advanced: DPC = 14.0 ± 2.81 days; control: DPC = 13.13 ± 3.41 days; delayed: DPC = 12.0 ± 1.34), indicating that parent barn swallows did not adjust the DPC to the altered timing of the brood, nor to the declining environmental conditions in second broods.

SELECTION FOR TIMING OF FLEDGING AND DURATION OF CARE

The differential survival of barn swallow fledglings resulted in a deviation from the average fledging date and DPC in the cohort of survivors (Fig. 3). Survivors fledged 1.4 days earlier and received 1 day longer DPC than the population average. In years with favourable autumnal food supply, there was no selection for fledging date, whereas selection for breeding early was strong in years with scarce autumnal food situations. In contrast, selection differentials for DPC were more pronounced in years with high autumnal food supply than in years with adverse autumns.

Discussion

The cross-fostering experiment revealed that differences in the post-fledging survival between second brood chicks reared by early and late pairs could not be explained by differences in the competence of the pairs. By contrast, a seasonal decline in post-fledging survival was observed in the chicks of all pairs irrespective of the treatment. Furthermore, the considerable variation of post-fledging survival between years confirms that the environmental conditions rather than the pair's rearing ability were the main determinants of the decline in juvenile survival. These results support the *date hypothesis*. The most important environmental factors for the reproductive performance and survival in aerial insectivores are the weather conditions, which strongly influence the food supply (Bryant 1975; Turner 1982; Turner 1983; Jones

1987; Martin 1987, McCarty & Winkler 1999). The annual variation in the decline in the estimates of airborne insects late in the season i.e. July to September was related to the post-fledging survival of barn swallows: in years with a scarce autumnal food supply selection favoured early fledging. In years with favourable conditions there was no selection for fledging date.

The occurrence of maternal effects or an altered nutritional state of females due to the prolonged or shortened incubation might confound the results of the clutch swapping experiment to favour the *date hypothesis* (Wardrop & Ydenberg 2003). However, experimental pairs being forced to prolong incubation of eggs (of potential lower quality) succeeded in raising nestlings to a better condition early in the nestling period (M. U. Grüebler & B. Naef-Daenzer, unpublished data). Also, the between-year variation in the slopes of the seasonal trends could not be explained by physiological factors. We therefore conclude that the support for the *date hypothesis* in the post-fledging period is only marginally due to confounding effects of the experimental manipulation. Nonetheless, we cannot preclude any additional effect of a seasonally declining parental rearing competence on the survival rate of second broods. Although the second brood season lasts for about two months, the maximum shift in the fledging date possible in this type of cross-fostering experiment is 10–12 days, since the eggs have to be exchanged during the incubation period. Therefore, the experiment could only include pairs that bred relatively simultaneously. Thus, further investigation is required to clarify potential effects of the parents' competence in second broods.

Our results indicate that the timing of breeding and the timing of the family break-up are temporal breeding decisions with immediate consequences on juvenile survival and thus, fitness. There was strong selection for long post-fledging parental care, especially in years with no steep decline of the food supplies. Therefore, we suggest that the benefits of longer post-fledging care depend on the environmental conditions and are greatest when food supply is high. On the other hand, the duration of care was not related to date. So it cannot be a causal or compensating factor in the seasonal decline in juvenile survival. Put together, these results indicate that the reproductive output is affected by temporal reproductive decisions on both the pre-fledging and the post-fledging period, and that these decisions are not necessarily related to each other. We believe that the decisions that are relevant for the post-fledging phase of reproduction are important components of the reproductive ecology of altricial birds, especially in multi-brooded species breeding in seasonal environments and being exposed to strong time constraints.

In conclusion, differential fledgling survival in relation to timing decisions in the post-fledging period is an important, although largely ignored, part of the selective mechanisms shaping the reproductive system of barn swallows. The decision when to start breeding, however prominent, is only one of the many decisions taken throughout the annual breeding cycle. This study shows that many of the consequences of these decisions are expressed in the post-fledging period. Therefore, to fully understand avian reproductive strategies and life histories, we suggest the need for an integrative approach to the fitness-relevant mechanisms operating in the entire reproductive cycle.

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Table 1. Food supply for second broods in the four study years based on daily insect estimates of 78 days between 15 July and 30 September. There was a significant variation in the mean number of flying insects $(3\ min)^{-1}\ m^{-3}$ and in the slope of the decrease in insect density ($F_{7,304} = 43.33$, $P < 0.001$, $R^2 = 0.488$; year: $F_{3,304} = 5.47$, $P = 0.001$; date: $F_{1,304} = 285.09$, $P < 0.001$; date*year: $F_{3,304} = 4.93$, $P = 0.002$). Autumnal food supply was categorized by the steepness of the slope (slope > -0.3: favourable; slope < -0.3: scarce).

Year	Mean insects ± SD	Slope ± SE	Autumnal food supply
2000	20.63 ± 10.60	-0.219 ± 0.050	Favourable
2002	20.52 ± 11.19	-0.336 ± 0.046	Scarce
2003	21.07 ± 11.10	-0.283 ± 0.048	Favourable
2004	22.70 ± 11.30	-0.464 ± 0.046	Scarce

Table 2. Model selection for post-fledging reencounter probabilities of barn swallows. For each model, the deviance (DEV), number of parameter (np), the modified Akaike's Information Criterion (QAICc) and the QAICc-deviation to the best model (ΔQAICc) are given. For all models an overdispersion factor ĉ = 1.277 was used. Model notation: Φ: survival probability; p: encounter probability; DPC = duration of post-fledging parental care; +: additive effect. For all reencounter models the modelling of the survival probability was kept constant $\Phi_{(age)}$.

Model	QAICc	ΔQAICc	np	DEV	Model description
1 $\Phi_{(age)} p_{(date+DPC+year+age)}$	2205.03	0.00	28	2148.44	Reencounter probability varies in relation to fledging date, DPC, year and age
2 $\Phi_{(age)} p_{(DPC+year+age)}$	2229.18	24.15	27	2174.64	Reencounter probability varies in relation to DPC, year and age
3 $\Phi_{(age)} p_{(year+age)}$	2251.35	46.32	26	2198.84	Reencounter probability varies in relation to year and age
4 $\Phi_{(age)} p_{(year)}$	2404.33	199.30	16	2372.13	Reencounter probability varies between years

Table 3. Model selection for post-fledging survival probabilities of barn swallows. For each model, the value of deviance (DEV), number of parameter (np), the modified Akaike's Information Criterion (QAICc) and the QAICc-deviation to the best model (ΔQAICc) are given. For all models an overdispersion factor ĉ = 1.277 was used. Models including the interactions between treatment and year and between treatment and date are not shown, since they were not favoured by model selection. Model notation: Φ = survival probability; DPC = duration of post-fledging parental care; +: additive effect; *: interaction. For all survival models the model structure of age-dependent survival and the whole reencounter model was kept constant (reencounter model: $p_{(date+DPC+year+age)}$; see Table 2).

	Model	QAICc	ΔQAICc	np	DEV	Model description
1	$\Phi_{(date*latefood+DPC+year+age)}$	2182.55	0.00	31	2119.84	*Date hypothesis*. Survival varies in relation to fledging date, DPC and food supply of the year; the slope of the seasonal decline differs between years with high and low food supply.
2	$\Phi_{(date+DPC+year+age)}$	2185.34	2.78	30	2124.66	*Date hypothesis*. Survival varies in relation to fledging date, DPC and food supply of the year.
3	$\Phi_{(treatment+date*latefood+DPC+year+age)}$	2185.63	3.07	33	2118.81	*Parental quality hypothesis*. Survival varies in relation to experimental treatment, fledging date, DPC and food supply of the year; the slope of the seasonal decline differs between years with high and low food supply.
4	$\Phi_{(treatment+date+DPC+year+age)}$	2188.02	5.46	32	2123.26	*Parental quality hypothesis*. Survival varies in relation to experimental treatment, fledging date, DPC and food supply of the year.
5	$\Phi_{(date+year+age)}$	2188.23	5.68	29	2129.60	*Date hypothesis*. Survival varies in relation to fledging date and food supply of the year.
6	$\Phi_{(treatment+date+year+age)}$	2189.37	6.82	31	2126.66	*Parental quality hypothesis*. Survival varies in relation to experimental treatment, fledging date and food supply of the year.
7	$\Phi_{(year+age)}$	2197.38	16.87	28	2140.80	No seasonal trend. Survival probability varies in relation to the food supply of the year.
8	$\Phi_{(DPC+year+age)}$	2198.21	17.70	29	2139.58	No seasonal trend. Survival probability varies in relation to DPC and food supply of the year.
9	$\Phi_{(DPC+age)}$	2202.59	22.08	28	2143.96	No seasonal trend. Survival probability varies in relation to DPC.

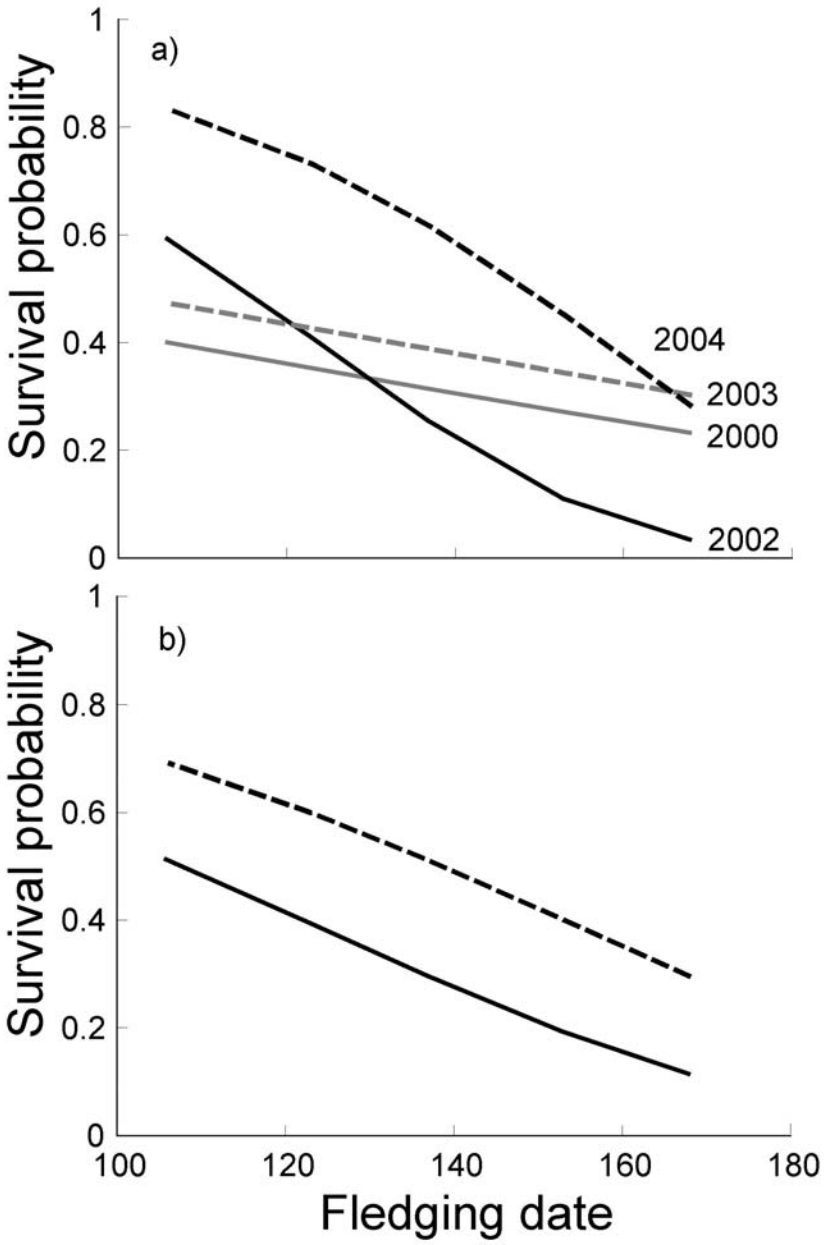

Fig. 1. Predicted values of the cumulative survival probabilities three weeks post-fledging as calculated using the best survival model (Table 3). (a) Differences among the four study years. The individual covariate "duration of parental care" (DPC) was set to the mean value (± SD) 13.15 ± 3.05 days. (b) Difference between two values of DPC (bold line = 9 days DPC; dotted line = 18 days DPC). Annual differences are not shown since annually different food supply and date effects were set to the mean value over the four years.

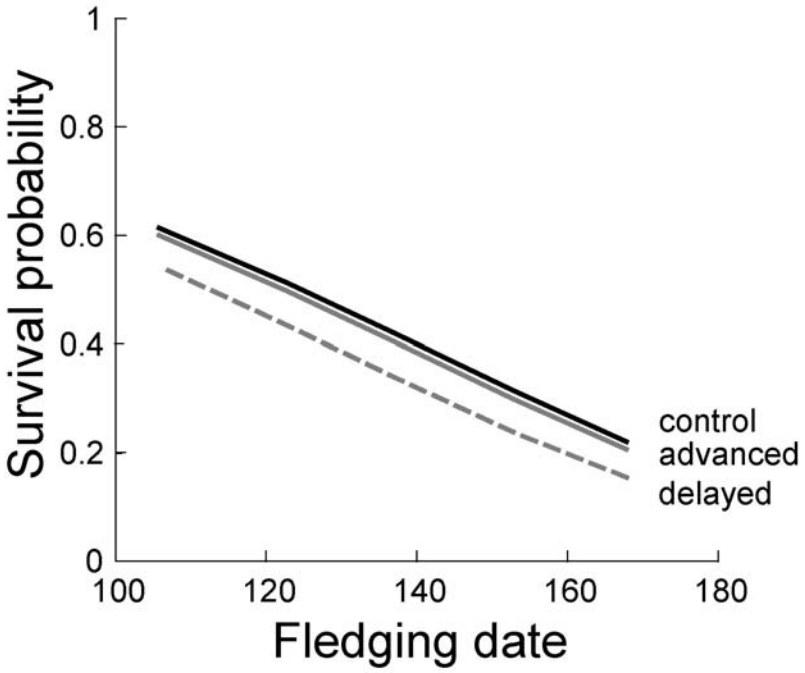

Fig. 2. Predicted values of the cumulative survival probabilities three weeks post-fledging for the experimental groups as calculated using survival model 3 (Table 3), which is the best model including a treatment effect. Other variables were set to the mean value.

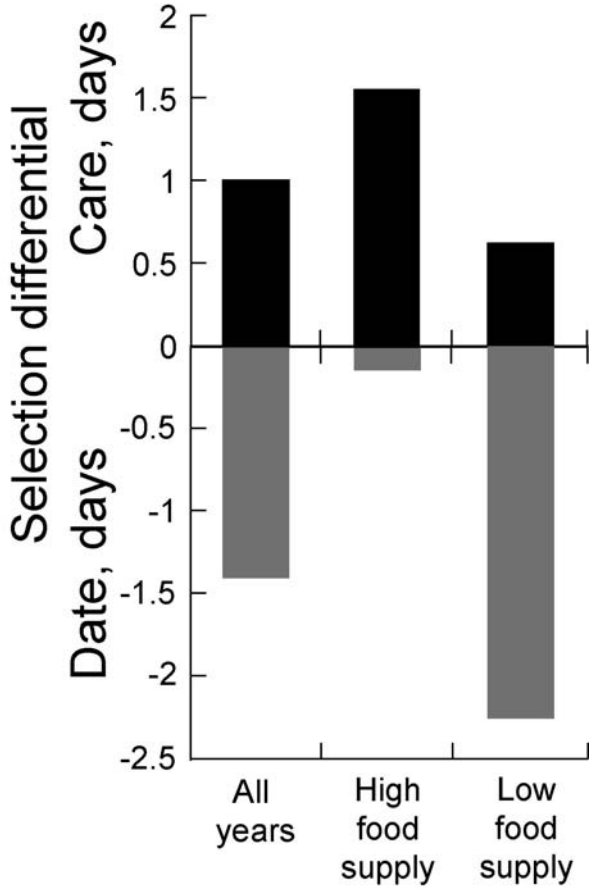

Fig. 3. Selection differentials in relation to autumnal food supply for fledging date and the duration of post-fledging care (DPC), respectively. The selection differential is the average value (fledging date or DPC) of surviving fledglings minus the population average (n = 97 survivors of 243 fledglings). Selection differentials indicate selection for early fledging and for long DPC. In years with scarce autumnal food supply selection for early fledging was more pronounced, whereas selection for a long DPC was less distinct than in years with favourable food supply.

CHAPTER 4

Fitness consequences of post-fledging parental investment: an experimental approach

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Abstract

Individual variation in parental investment is a key determinant of differential reproductive output in species with parental care. Although most passerine birds continue to care for their young beyond fledging, investigations of this important issue are restricted to the pre-fledging period. Here, we analyse the survival of juvenile barn swallows in relation to the duration of post-fledging parental care. To disentangle the direct effect of post-fledging investment from pre-fledging effects, we conducted a partial cross-fostering experiment, manipulating the duration of post-fledging care. We used radio-tracking and colour marks to monitor the juveniles after leaving the nest and we applied AIC model selection to compare pre-defined Cormack-Jolly-Seber survival models. We found a strong positive effect of the duration of post-fledging parental care on both the over-all juvenile survival and the timing of the survival depression occurring upon family break-up. Long parental care improved the juveniles' survival in the first 3 weeks post-fledging and flattened the survival depression after family break-up. Independent of the period of post-fledging care, juveniles originating from parents with high post-fledging investment had higher survival rates compared to chicks originating from short-care pairs. This component of variation in post-fledging survival was probably due to differences in the parents' efforts during the nestling period. The results show that the extent of post-fledging parental investment is an important reproductive trait, accounting for a large proportion of differentials in post-fledging survival, and therefore is highly relevant for understanding avian life-history evolution and breeding strategies.

Introduction

Life-history theory predicts that the parents' investment of time and energy in reproduction is adjusted to maximise the number of recruits into the population (Clutton-Brock 1991). In birds, there is, for example, a strong relationship between parental feeding rates, the growth rate of nestlings and their subsequent survival (overview in Newton 1989). Although most altricial birds provide intense care for their chicks beyond fledging, investigations of the costs and benefits of avian parental investment are restricted to the pre-fledging period due to the difficulties involved in monitoring bird fledglings (Smith 1978; Weatherhead & McRae 1990; Ogden & Stutchbury 1997; Wheelwright, Tice & Freeman-Gallant 2003).

During the first weeks after leaving the nest, young birds face a high mortality risk (Anders *et al.* 1997; Naef-Daenzer, Widmer & Nuber 2001a; Götmark 2002; Kershner, Walk & Warner 2004) because they lack crucial life skills (Davies 1976; Marchetti & Price 1989; Wheelwright & Templeton 2003; Yoda, Kohno & Naito 2004). Poor post-fledging survival of inexperienced juveniles may be due to both insufficient food intake or high predation risk in the absence of the parents (Sullivan 1989; Götmark 2002). Parental post-fledging care could mitigate the high mortality risk after fledging (Martin 1996; Badyaev 1997). Consequently, the extent to which parent birds continue to care for fledglings is probably a fitness-relevant trait (Verhulst, Tinbergen & Daan 1997; Webb *et al.* 2002) and, thus, an important aspect of avian breeding strategies and life histories (Russell 2000; Cam, Monnat & Hines 2003; Wheelwright *et al.* 2003).

Here, we use the barn swallow (*Hirundo rustica)* as an example organism and the duration of post-fledging care as an estimate of the intensity of investment to test direct effects of the parents' post-fledging investment on juvenile survival. We present a partial cross-fostering experiment to analyse i) whether the duration of post-fledging care has an effect on the survival of juveniles in the first 21 days after fledging, and ii) the importance of this effect compared to pre-fledging factors that also affect post-fledging survival. The resulting differences in offspring survival quantify the fitness consequences of the variation in the duration of the parent's post-fledging care.

Materials and methods

The experiment was carried out in 2002 and 2003 in a farmland plain of approximately 20 km^2 near Lucerne, Switzerland (47°10' N / 8° 02' E). Only first broods were cross-fostered. All barn swallow nests at 60 farms were visited weekly to record new clutches. At the end of the

incubation period, the nests were inspected daily to determine the exact hatching date (= date when the first egg hatched). The hatching date was considered to be day 1 of the nestling period. On average, the chicks fledged at an age of 21.77 days ± 1.17 SD. Nestling survival was high (0.94 ± 0.19 SD), whereas the mortality during the post-fledging period was substantial.

EXPERIMENTAL PROCEDURE

To manipulate the duration of post-fledging parental care (DPC) and to separate pre-fledging from post-fledging effects, we conducted a partial cross-fostering experiment. Broods with equal hatching date (± 1) and equal number of fledglings (± 1 on nestling day 19) were selected as experimental broods. Half of the nestlings were exchanged between nests when they were close to fledging (brood size of 3 or 4: 2 nestlings exchanged; brood size of 5 or 6: 3 nestlings exchanged). Individual nestlings were ranked according to their body mass within the original brood and only nestlings of equal rank were exchanged. Due to the high variability of DPC, cross-fostered fledglings experienced, in most cases, a shorter or longer period of post-fledging care compared to their siblings in the original brood. Thus, the procedure created 4 experimental groups: (1) long-care fledglings, originating from parents providing long care (= *naturally long care*, control group 1) (2) long-care fledglings, originating from parents providing short care (= *prolonged care*) (3) short-care fledglings, originating from parents providing short care (= *naturally short care*, control group 2) (4) short-care fledglings, originating from parents providing long care (= *shortened care*).

Cross-fostering was performed in 21 sets of two broods (2002: 11 sets, 2003: 10 sets) and succeeded in 18 sets. In two cases, the pairs did not differ in DPC. According to the observed DPC, the fledglings of these four families were assigned to the group *naturally long care*. In one set, one pair lost all juveniles and the DPC could not be estimated. The non-experimental fledglings of the remaining family were included in the experimental group *naturally long care*. Additionally, the tagged fledglings of 8 families without nestling exchange were included in the *naturally long care* control group. The sample sizes for each group are given in Table 1.

JUVENILE TREATMENT

The juvenile swallows were caught at their nests during the night of nestling day 19 or 20. To record their body development and condition, we measured the length of the third primary

feather to the nearest 0.5 mm and scored the fat reserves (scores 0–4) by estimating the extent of subcutaneous fat deposits at the abdomen based on (Kaiser 1993). The juveniles were weighed to the nearest 0.5 g. All chicks were radio-tagged with a miniature transmitter of own construction with a life of 3 to 5 weeks and a range of 2 to 5 kilometres (Naef-Daenzer 1993; Naef-Daenzer *et al.* 2005). The complete radio-tag had a mass of 650 to 750 mg, i.e. maximally 4.4 % of the mass of the lightest fledgling (17 g). The transmitters were attached using a Rappole-type harness made from 0.5 mm elastic cord (Rappole & Tipton 1990). To detect eventual loss or failure of transmitters, all juveniles were individually colour-marked on the light plumage of the belly. A combination of two out of four colours (green, blue, red, none) was applied using waterproof felt pens (Edding 3000®). These patterns occurred repeatedly among families and were complemented by a family-specific pattern. A pilot study in 2000 revealed no measurable differences in behaviour, flight activity, and manoeuvrability or in the survival between radio-tagged juveniles and a control group of colour-marked but untagged fledglings (own unpublished data). For a detailed test of eventual adverse effects of radio-tagging on small birds, see also Naef-Daenzer, Widmer & Nuber (2001b). After radio-tagging, the juveniles were put in the nests of either their original or the foster parents and the nest cups were closed using a flexible plastic cover to prevent premature departure. We then waited 5–10 minutes until the birds had relaxed and removed the covers in complete darkness.

RADIO TRACKING AND BEHAVIOURAL DATA

All birds were located twice per day. The observation sessions lasted one hour and included the recording of feeding rates as an estimate of the intensity of the post-fledging care. Particular care was given to avoid errors in monitoring survival (e.g. denoting dead birds with a working transmitter as alive, or live birds with a broken transmitter as dead). Missing birds were searched up to an age of 40 days post-fledging within an area of approximately 100 km^2 from fixed antenna stations at selected vantage points and using vehicles equipped with an omni-directional antenna. Additionally, flocks of swallows in this area were searched to detect birds with colour-marks. All telemetry and visual observations were used to create daily encounter histories for the analyses of survival and re-encounter probabilities. The duration of post-fledging parental care (DPC) of a family was defined as the period from the day of fledging to the day of the last food delivery to the fledglings observed.

STATISTICAL ANALYSIS

Our data on feeding rates had a hierarchical structure with the observation session nested within pairs. To take into account the variation among pairs, we included the nested effect of pairs as random factors into a linear mixed model, using the restricted maximum-likelihood (REML) method (Patterson & Thompson 1971) in Genstat 5, release 9.1. Parental feeding rates declined non-linearly with chick age since fledging. Hence, we used a third-order polynomial as covariates and the DPC as a fixed factor (long care, short care). We also included the interaction between age and DPC. These fixed effects were tested with the Wald test (Dobson 1990).

To analyse post-fledging survival, we used Cormack–Jolly–Seber mark-recapture models (Lebreton *et al.* 1992; Anderson & Burnham 1994) in the software package MARK (White & Burnham 1999), allowing separate estimation of the re-encounter rate (p) and the survival rate (Φ). For all fledglings in a brood, the fledging day was the first occasion of the encounter-history. Analyses were based on the individual encounter histories, covering 9 periods of 2–10 days each (day 1–2; 3–5; 6–8; 9–11; 12–14; 15–17; 18–21; 22–28; 29–38). On one hand, pooling reduces the number of parameters to estimate and thereby increases the likelihood of estimating all of them. On the other hand, pooling may introduce a bias in the parameter estimates if the degree of pooling is high and re-encounter and survival probabilities are low (Hargrove & Borland 1994), which was not the case for the first 3 weeks of the post-fledging period.

A goodness-of-fit test of the most general model without covariates $\Phi_{(\text{origin+DPC*age})}$ $p_{(\text{year*age})}$ was performed with a parametric bootstrap (100 simulations). The observed deviance (dev = 1590.48) did not differ significantly from the simulated deviances (mean dev = 1562.31 ± 8.16 SE ; p = 0.31), indicating that this model adequately fitted the data. Although survival probability of siblings was shown to be statistically independent (e.g. Hochachka 1990; Naef-Daenzer *et al.* 2001a) a biological reason for overdispersion in mark–recapture models may be the lack of independence between individuals of the same original brood. Overdispersion reduces the variance of parameter estimates and can therefore bias the model selection, but point estimates of the parameters remain unbiased (McCullagh & Nelder 1989; Anderson & Burnham 1994). We estimated the overdispersion factor from the GOF test ($\hat{c}$ = 1.103) and adjusted variances of the parameters and model selection criteria (Akaike Information Criterion, QAICc) accordingly (Burnham & Anderson 1998). The model with the smallest QAICc value was chosen to make inferences about the outcome of the experiment.

CANDIDATE MODELS

A set of 6 candidate models was defined a priori, which allows powerful inferences after model selection ((Burnham & Anderson 1998); see Table 2). Since the cross-fostering experiment separates the effects of pre-fledging factors (related to DPC) from the effect of DPC, 4 possible outcomes were hypothesised. (i) The experimental groups do not differ in post-fledging survival. Juvenile survival depends neither on DPC nor on associated pre-fledging factors (Table 2, model 1). (ii) Post-fledging survival depends exclusively on pre-fledging factors. Parents providing long care produce more viable fledglings whose survival prospects are high regardless of the DPC. Foster chicks will not differ in their survival from their siblings remaining in the original nest (Table 2, model 2). (iii) Post-fledging survival depends exclusively on DPC. At fledging, the viability of offspring does not differ between pairs providing long and short care. We therefore expect differential survival in relation to DPC, but no within-brood difference in the survival of original and foster chicks (Table 2, model 3). (iv) Post-fledging survival depends on DPC as well as on pre-fledging factors. We expect differential survival in relation to DPC and a within-brood difference in the survival of original and foster chicks related to their origin. E.g. prolonging DPC is expected to improve post-fledging survival, but not to the rate in the *naturally long care* group (Table 2, model 4). Furthermore, all models included effects of age (days post-fledging, 9 categories). Two further models were added to the candidate model set. Both models incorporating an effect of DPC were complemented by the interaction between DPC and age. These models test for differences in the age-related survival pattern between short-care and long-care fledglings. If DPC determines post-fledging survival, we might expect a survival depression after family break-up and the timing of the depression would be related to DPC (Table 2, model 5 & model 6). All the candidate models used the same modelling of re-encounter probability including differences in relation to age (post-fledging), year (type of telemetry transmitter) and DPC ($p_{(DPC+year*age)}$).

The cross-fostering manipulation just before fledging was feasible because parent barn swallows do not recognize their young by individually distinctive cues in this stage (Medvin 1986). However, barn swallow chicks are able to recognize their parents, which may introduce an adverse effect of the experimental manipulation. Foster juveniles might suffer from the exchange, and thus have lower survival (groups *prolonged care* and *shortened care)*. To test if exchanging chicks did bias the results, we added post-hoc the modelling of survival differences between exchanged and unexchanged fledglings to the best survival model.

Results

The average duration of post-fledging parental care (DPC) differed significantly between short-care (7.56 days ± 1.25 SD, n = 18) and long-care pairs (11.71 days ± 2.21 SD, n = 31; $F_{1,47} = 53.44$, $P < 0.001$). Within the experimental group *naturally long care*, we did not find a difference in DPC between the additional long-care pairs (12.38 days ± 2.60 SD; n = 13) and the experimental long-care pairs (11.22 days ± 1.80 SD; n = 18; $F_{1,29} = 53.44$, $P = 0.151$). On average, the DPC of exchanged juveniles was prolonged or shortened by 3.67 days (SE = 0.52, range 1–7 d) compared to their unexchanged siblings. The broods (including foster juveniles) did not differ in the age of nest departure (short-care pairs: nestling day 22.09 ± 1.20 SD, n = 18; long-care pairs: nestling day 21.58 ± 1.12 SD, n = 31; $F_{1,47} = 2.26$, $P = 0.14$). Consequently, the difference in the duration of post-fledging care between the experimental pairs was not caused or biased by a difference in the duration of the nestling period.

The mean fledging condition of the original nestlings of short-care and long-care pairs did not differ (multivariate GLM: Wilks' Lamda = 0.954, P = 0.539, n = 49). There were no differences in the mean length of the third primary feathers ($F_{1,47} = 0.102$, $P = 0.751$), the body mass ($F_{1,47} = 1.221$, $P = 0.275$) or the birds' fat deposits ($F_{1,47} = 0.216$, $P = 0.645$). Accordingly, we could not find any differences in the fledging condition between the 4 experimental groups (multivariate GLM: Wilks' Lamda = 0.647, P = 0.756, n = 84).

Long and short caring pairs differed significantly in the pattern of feeding behaviour after fledging of their brood. At first, in the first five days post-fledging, the feeding rates per chick per hour did not differ significantly (Table 3, Fig. 1). However, from day 6 onward, long-care pairs supplied an increasingly larger proportion of feedings. Overall, the long-care pairs supplied c. 146 % of the amount supplied by short-care pairs. This indicates that a short DPC represents a smaller post-fledging investment of time and energy, and that the short duration of care was not compensated by an elevated rate of feedings.

Model selection favoured the model including both, the effect of DPC and the effect of origin over the model considering only the effect of DPC (Table 4). Post-fledging survival was enhanced by a long DPC and by pre-fledging factors associated with long-care pairs. Furthermore, the two best models showed differences in the age-related survival pattern between short-care and long-care fledglings (Table 4). These differences were expressed by a different shape of the survival depression which occurred during the first days after family break-up (Fig. 2). The experimental manipulation of DPC shifted the survival depression in time and altered its amplitude. In long-care fledglings the survival depression was later and

more moderate compared to short-care fledglings (*naturally long* and *prolonged care*: depression at days 15–17, *naturally short* and *shortened care*: depression at days 12–14; Fig. 2). Shortening of DPC advanced and deepened the low of the depression in daily survival (*naturally long care*: $\Phi = 0.937$ (SE = 0.025); *shortened care*: $\Phi = 0.896$ (SE = 0.033); Fig. 2), whereas prolonging care delayed and flattened the low (*naturally short care*: $\Phi = 0.854$ (SE = 0.043), *prolonged care*: $\Phi = 0.909$ (SE = 0.036); Fig. 2). To estimate the reproductive output of the four experimental groups we calculated the cumulative survival over the first 3 weeks post-fledging for each of the group (Fig. 3). Prolonging care increased cumulative survival probability over the first 3 weeks, whereas shortening of DPC decreased the cumulative survival probability, indicating that an early family break-up decreased the reproductive output of a breeding attempt. In addition, fledglings with *naturally long care* experienced an increased cumulative survival compared to long-care fledglings originating from short-care pairs (*prolonged care*). This result revealed an adverse effect of pre-fledging factors in fledglings originating from short-care pairs (Fig. 3). Conversely, short-care fledglings originating from long-care pairs (*shortened care*) experienced increased survival when compared with fledglings with *naturally short care* (Fig. 1, Fig. 2). The effect size of origin was b = 0.384 (SE = 0.211).

To consider the potential bias that might occur in the survival probability of exchanged fledglings compared to their unexchanged siblings (effect of manipulation), an additional exchange parameter was added post-hoc to the best model ($\Phi_{(\text{exchange+origin+DPC*age})}$). However, this model was not favoured by the model selection (QAICc = 2727.4, ΔQAICc = 1.42, np = 32, deviance = 2662.57). From the results on the post-fledging feeding rates we expect that short-care fledglings and long-care fledglings do not differ in the post-fledging survival of the first 5 days post-fledging. In a post-hoc procedure, we therefore rebuilt the two best models including an effect of DPC that started not until day 6 post-fledging. These models were favoured by the model selection ($\Phi_{(\text{origin+DPC*age})}$: QAICc = 2723.7, np = 30, deviance = 2663.03; $\Phi_{(\text{DPC*age})}$: QAICc = 2725.35, np = 29, deviance = 2666.69), indicating that a short DPC affects offspring survival not before day 6 post-fledging.

Discussion

A long period of post-fledging parental care is a considerable investment into current reproduction in terms of time and energy that otherwise could be allocated to alternative functions such as maintenance or another breeding attempt. To our knowledge, this is the first

study to quantify the direct effects of the duration of post-fledging parental care on juvenile survival. The period during which barn swallow parents cared for their chicks varied considerably, and the experimental change in the duration of care had a severe effect on the survival of juveniles. In fact, it accounted for about half of the variation in post-fledging survival amongst the experimental groups. These results demonstrate that the decision how long parents care for their fledglings has direct consequences on the pair's reproductive output.

The time immediately after family break-up coincided with a noticeable depression in juvenile survival. Pairs that provided a long post-fledging care experienced a late and moderate low in the juvenile survival depression, whereas in short-care pairs the low occurred early and was deepened. An early timing of family break-up results therefore in decreased survival prospects of the newly independent juveniles. Seen from the perspective of juveniles, parental care should last up to the time when juveniles no longer experience increased mortality risk, having received sufficient food to cover their high energy requirements and having obtained better manoeuvrability skills to escape predation. However, parents stopped caring for their fledged juveniles before they fully developed the essential life skills. Considering these results and that of studies on fledgling flight proficiency (Weathers & Sullivan 1989; Weathers & Sullivan 1991) we suggest that a considerable parent-offspring conflict over the timing of family break-up exists (Godfray 1995; Arroyo, De Cornulier & Bretagnolle 2002). The parental decision to reduce the duration of post-fledging care and to risk the associated fitness costs might be due to constraint or restraint mechanisms. Short-care pairs may experience energetic constraints and, as a result, invest only short time in reproduction because they need to allocate the available energy to self-maintenance. Alternatively, pairs providing short post-fledging care probably reduce investment in the current brood as they adjust their investment to the reproductive value of the brood, irrespective of the own energetic condition. In our study, the workload of short-care pairs was not reduced, since they started immediately with the second brood after the family break-up of the first (own unpublished data). Furthermore, double-brooded pairs provided shorter care to the fledglings of the first brood than single brooded pairs, indicating a trade-off between a long post-fledging care of the first brood and an early start of the second brood (own unpublished data). We therefore suggest that shortening post-fledging care is likely to be a breeding decision of parents maximizing the lifetime reproductive success rather than the result of an energetic constraint. However, to date, the factors affecting the duration of post-

fledging care remain largely unknown (Yoda *et al.* 2004), although intra-specific variation in the post-fledging time investment is widespread (Edwards 1985; Spear, Ainley & Henderson 1986; Geupel & DeSante 1990; Pöysä 1992; Székely *et al.* 1996; Verhulst & Hut 1996; Verhulst *et al.* 1997; Vega Rivera *et al.* 2000; Cam *et al.* 2003; Wheelwright *et al.* 2003). Quantifying the costs and benefits of parental investment after fledging is crucial for the understanding of individual breeding strategies and of the evolution of inter-specific differences in altricial life-histories (Martin 1996; Skutch 1996; Russell 2000; Badyaev & Ghalambor 2001; Russell, Yom-Tov & Geffen 2004; Schaefer *et al.* 2004).

In this study, post-fledging survival was additionally affected by unidentified pre-fledging factors. Chicks of long-care pairs had a markedly higher survival rate than chicks of short-care pairs, irrespective of the duration of care experienced. We conclude from the results that a similarly high proportion of the variation in post-fledging survival was determined by the origin of the chicks. Our data do not allow us to analyse which pre-fledging factors (heritable traits, maternal effects or parental investment in nestlings) were responsible for these differences. Since the chicks of the experimental groups did not differ in their physical condition or body size, differential feeding regimes are an unlikely explanation for the differences in post-fledging survival. Proximately, the main reason for juvenile mortality after fledging was predation by raptors, which is in agreement with previous studies (e.g. Sullivan 1989; Anders *et al.* 1997; Naef-Daenzer *et al.* 2001a; Götmark 2002; Kershner *et al.* 2004)). Thus, we suspect that the chicks' physiological and energetic competence (Simon *et al.* 2004; Moreno *et al.* 2005; e.g. foraging and flight competence) or behavioural characteristics such as predator vigilance (Cresswell *et al.* 2003; Lind 2004) might be of crucial importance for surviving the first post-fledging weeks. The pre-fledging determinants of such behavioural traits remain widely unknown.

Higher survival of long-care fledglings might not only result from the longer period of care, but also from a higher quality or intensity of the post-fledging care provided by long-care pairs. The analysis of post-fledging feeding rates did not support this idea. Long-care pairs and short-care pairs fed at an equal rate in the first days post-fledging. We therefore suggest that the maintenance of care prevents from increased mortality rather than the intensity of care. However, in total, long-care fledglings received considerably more food from the parents after fledging compared to short care fledglings. Hence, short parental care was not compensated by a high intensity of care.

Parent swallows might adjust post-fledging investment to the changing reproductive value of the brood, if fledglings die before the family break-up (Winkler 1991; Pöysä 1992). Consequently, the duration of care and the outcome of the experiment are possibly affected by juvenile mortality before independence, leading to a shorter care period in broods with a low number of surviving fledglings. Yet, the survival depression occurred after family break-up and therefore we are confident that the duration of care is a main determinant of post-fledging survival, even if post-fledging investment was influenced by the juvenile mortality before family break-up.

In conclusion, we show that the parental decision regarding the duration of post-fledging care has an immediate and marked effect on juvenile survival, irrespective of pre-fledging factors, and that the duration of care is therefore a key component in the survival of a brood. The parental post-fledging investment is identified as an important but so far widely neglected factor in breeding strategies, and might be crucial to our understanding of life-history evolution in altricial bird species. Differences in the reproductive value of broods are likely to influence the post-fledging investment, thereby affecting the reproductive output of individual pairs, populations and species. We assume that parental post-fledging investment has coevolved with interrelated fitness-relevant life-history traits, such as clutch size, multi-broodedness and adult survival, and that it represents an important part in the fecundity–survival patterns, which maximize the fitness in a given environment.

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Table 1. Sample sizes of the experimental groups. Half of the fledglings were exchanged between two families of the same age just before fledging. Due to variation in the duration of post-fledging parental care, the exchanged fledglings received shortened or prolonged care when compared to their unchanged siblings. The radio-tagged fledglings of additional families without manipulation were assigned to the group of "naturally long care". The numbers of radio-tagged families and fledglings in the two study years are given below.

		2002	2003	Total
Short care	Families	9	9	18
Naturally short care	Fledglings	24	24	48
Shortened care	Fledglings	19	19	38
Long care	Families	17	14	31
Naturally long care	Fledglings	48	46	94
Prolonged care	Fledglings	21	23	44
Total	Families	26	23	49
	Fledglings	112	112	224

Table 2. Candidate models, model notation and biological significance. Φ denotes post-fledging survival probability. Re-encounter probability was modelled in all candidate models with age and year effects as well as with an additive effect of DPC ($p_{(DPC+year*age)}$). DPC = experienced duration of post-fledging parental care ($DPC_{short\ care}$ = 7.56 days ± 1.25 SD; $DPC_{long\ care}$ = 11.71 days ± 2.21 SD); origin = originating from short-care or long-care pairs before cross-fostering; age = age-dependent post-fledging survival probability.

Model	Significance
1. $\Phi_{(age)}$	Age-dependent survival probability; no variation in survival probability according to origin or DPC
2. $\Phi_{(origin+age)}$	Survival probability differs according to the origin of juveniles, exclusive effect of pre-fledging factors
3. $\Phi_{(DPC+age)}$	Survival probability differs according to the DPC experienced, exclusive effect of DPC
4. $\Phi_{(origin+DPC+age)}$	Suvival probability differs according to both DPC and origin, combined effects of DPC and pre-fledging factors
5. $\Phi_{(DPC*age)}$	Survival probability differs according to the DPC experienced, showing an early survival depression in short-care fledglings and a late survival depression in long-care fledglings.
6. $\Phi_{(origin+DPC*age)}$	Survival probability differs according to both DPC and origin, showing a survival depression peak in short-care fledglings and a late survival depression in long-care fledglings.

Table 3. Fixed effects of fledgling age and group of care (long-care pairs, short-care pairs) on the post-fledging feeding rates (feedings per fledgling per h; $N = 804$ sessions) in barn swallows, tested in a linear mixed model analysis (REML; random model: year and sessions nested in pairs; deviance = 3135.16, df = 796). The effects of the factor "care" and its interaction with the fledgling age is given for long-care pairs (versus short-care pairs). The effects ± SE and Wald statistics are given with significance levels. Degree of freedom for all variables was 1.

Fixed effects	effects ± SE	Wald statistic	*P*
Fledgling age	2.113 ± 0.683	88.12	<0.001
(Fledgling age)^2	-0.469 ± 0.139	21.18	<0.001
(Fledgling age)^3	0.022 ± 0.008	7.23	0.007
Care (factor)	0.815 ± 0.514	2.22	0.137
Care*age	0.324 ± 0.110	8.70	0.003

Table 4. Results of the model selection among the 6 candidate models. Φ describes the survival probability, keeping re-encounter probability constant ($p_{(DPC+year*age)}$). DPC = experienced duration of post-fledging parental care; origin = originating from short-care or long-care pairs before cross-fostering, age = age-dependent juvenile survival probability. The modified Akaike Information Criterion (QAICc), the QAICc-deviation to the best model (ΔQAICc), the Akaike weight, the number of estimated parameters (np), and the deviance are given for each model. The most parsimonious model with ΔQAICc = 0 was used for inferences. Model selection was conducted using the overdispersion factor ĉ = 1.103.

Model	QAICc	ΔQAICc	Akaike weight	np	Deviance
$\Phi_{(origin+DPC*age)}$	2725.95	0.00	0.56	31	2663.19
$\Phi_{(DPC*age)}$	2727.36	1.40	0.28	30	2666.64
$\Phi_{(origin+DPC+age)}$	2729.61	3.65	0.09	27	2675.03
$\Phi_{(origin+age)}$	2731.79	5.83	0.03	26	2679.25
$\Phi_{(DPC+age)}$	2732.11	6.16	0.03	26	2679.57
$\Phi_{(age)}$	2733.89	7.94	0.01	25	2683.39

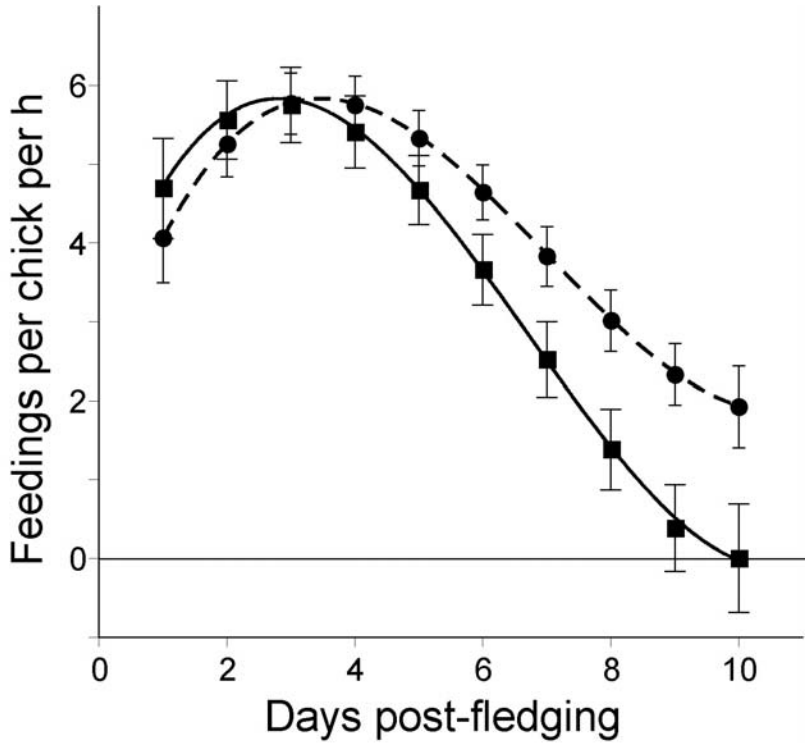

Fig. 1. Daily post-fledging feeding rates (± SE) of short-care pairs (solid line) and long-care pairs (broken line). Predicted values (feedings per chick per hour ± SE) in relation to the days since fledging are shown. Other significant variables (see Table 3) were kept constant at their means.

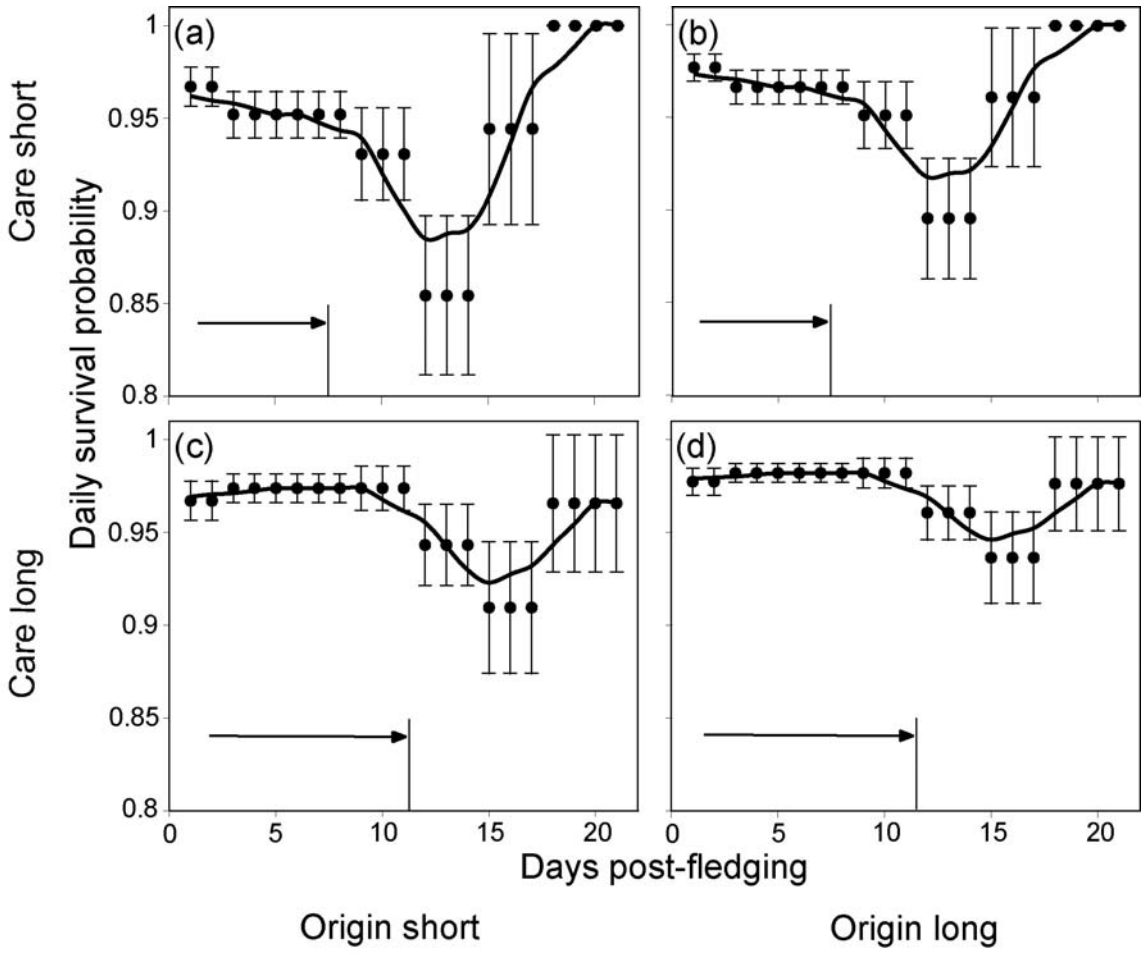

Fig. 2. Daily survival probabilities (± SE) during the first 3 weeks post-fledging for the 4 experimental groups determined by the best model (Table 4). Survival probabilities are calculated using Cormack–Jolly–Seber mark-recapture models and model selection was done by Akaike Information Criterion. (a) *Naturally short care:* short-care fledglings originating from parents providing short care, (b) *shortened care:* short-care fledglings originating from parents providing long care, (c) *prolonged care:* long-care fledglings originating from parents providing short care, and (d) *naturally long care:* long-care fledglings originating from parents providing long care. Arrows indicate the average duration of post-fledging parental care (DPC) of the corresponding groups.

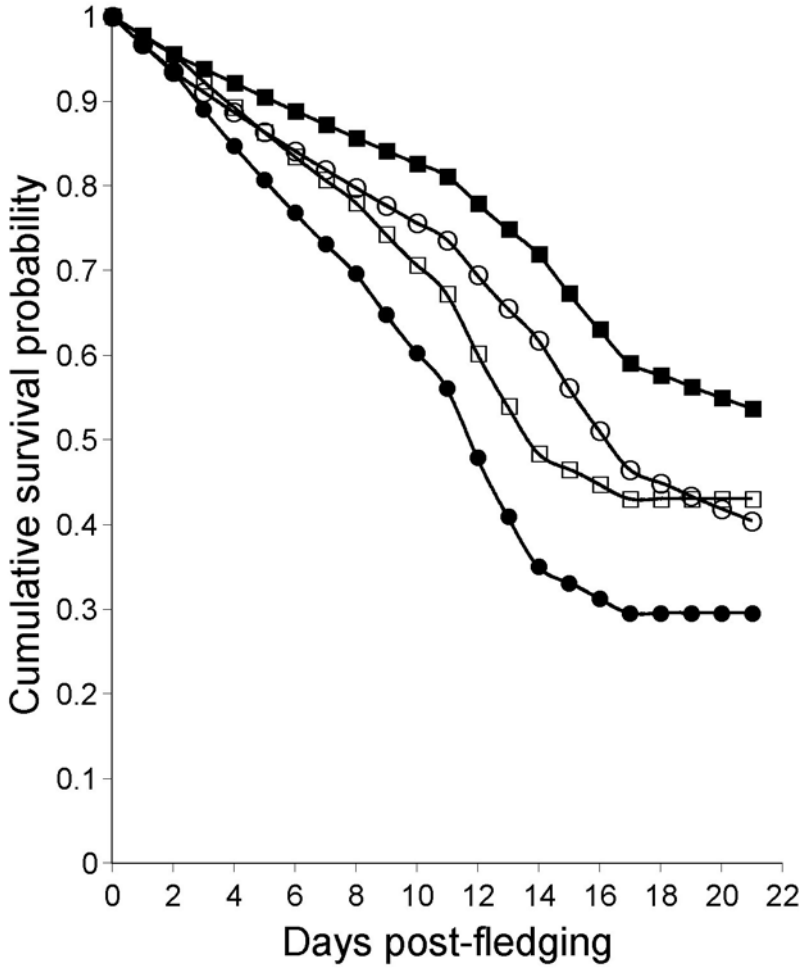

Fig. 3. Cumulative probability of juvenile barn swallow survival during the first 3 weeks post-fledging for the 4 experimental groups calculated using daily survival probabilities of the best model. Filled squares: *naturally long care*; open squares: *shortened care*; filled circles: *naturally short care*; open circles: *prolonged care*.

CHAPTER 5

Differential post-fledging parental investment in a multi-brooded passerine: a trade-off in the allocation of time

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Submitted to Animal Behaviour

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Abstract

In altricial birds, the importance of post-fledging parental care for variation in reproductive output is poorly understood due to the difficulty of following family groups after fledging. From an evolutionary perspective, post-fledging parental care should be terminated as soon as the benefits from deserting the young outweigh those from continuing parental care. In seasonal environments multiple breeders have to allocate time to several broods. They may trade-off the benefits of the time invested in the care of fledglings of one brood against the benefits of an advanced start of the subsequent clutch. Whether the allocation of time to different clutches is additionally affected by the timing of breeding and the intrinsic quality of pairs remains unknown. Using radio-telemetry of 494 fledglings in 114 families (n = 88 pairs) of the double-brooded barn swallow *Hirundo rustica*, we showed that the duration of post-fledging parental care is reduced in first broods (n = 51) by 29 % compared to single (n = 14) and second broods (n = 49). In second broods, feeding rate, but not the duration of investment was increased compared to single broods. Furthermore, the period of post-fledging care was considerably reduced in pairs with a late start of reproduction. The duration of post-fledging care was also related to the length of the female's tail streamer. These results are consistent with the hypothesis that barn swallows adjust the duration of post-fledging care in relation to future reproductive attempts due to an intra-seasonal trade-off in the allocation of time between successive broods. The outcome of this reproductive decision depends on the pair's timing and the female's state. We suggest that in multi-brooded altricial species the timing of family break-up is an adaptive reproductive decision to maximise lifetime reproductive output.

Introduction

Parental care is considered to be a trait adapted to maximize the parents' lifetime fitness. The decision on the extent of care is based on the benefits of the current investment in caring behaviour relative to its eventual costs in terms of survival or future reproductive success (Carlisle 1982; Winkler 1987; Clutton-Brock 1991). From an evolutionary perspective, parental care should be terminated when the benefits from deserting the young exceed the benefits of a continued care (Williams 1966; Stearns 1992; Székely *et al.* 1996). Most empirical studies investigating the underlying mechanisms of termination of care concentrate on the adjustments of parental investment according to the reproductive value of the current brood, since the value of a brood can be manipulated in brood size experiments ((Eadie & Lyon 1998; Pöysä & Milonoff 1999; Verboven & Tinbergen 2002; Ackerman *et al.* 2003). In contrast, investigations of investment decisions according to the expected future reproductive success are rare.

Multiple breeders in seasonal environments are adapted to have their clutches within the period in which environmental conditions are favourable. In this case, time may be a relevant currency of parental investment (Verhulst, Tinbergen & Daan 1997). Time investment can entail reproductive costs in future reproduction, as it delays the start of the next breeding attempt, shifting it closer towards the end of the season. This may, in turn, affect the reproductive value of the next brood due to declining environmental conditions (Martin 1987; Svensson 1997; Nilsson 1999). Early termination of care may be advantageous to renesting pairs because an advanced start of the subsequent brood may result in increased juvenile survival (Kluyver, van Balen & Cavé 1977; Verhulst & Hut 1996; Verhulst *et al.* 1997). The benefits of an advanced start of the next brood is likely to increase in the course of the season until the costs of a next breeding attempt outweigh its benefit and pairs refrain from renesting. Intrinsic parental factors such as the physiological competence might play an additional role in intra-seasonal trade-offs between successive broods. Energetic constraints may delay the start of the next breeding attempt or reduce the investment into the next brood (Thompson 1992). Moreover, reproductive investment in the current breeding season might be reduced, if the survival prospects of breeders are enhanced by a high competence and condition (Clutton-Brock 1991; McNamara & Houston 1996; Webb *et al.* 2002).

Altricial birds can adjust their current reproductive effort by varying the size of the clutch. Thereafter, they have limited opportunities to vary the investment in time and energy until the brood has fledged (except brood desertion). Options to adjust efforts exist after

fledging when parents can vary both the duration and intensity of care. However, the duration of parental care and the causes for its variation still are poorly understood, since it becomes increasingly difficult to follow family groups after fledging and to observe interactions between fledglings and their parents (Naef-Daenzer, Widmer & Nuber 2001a; Wheelwright, Tice & Freeman-Gallant 2003). Hence, a potentially critical period of avian parental investment has been ignored so far, namely the parental care of young from fledging to independence (Evans Ogden & Stutchbury 1997; Vega Rivera *et al.* 2000; Wheelwright *et al.* 2003). Since the total duration of care of a breeding attempt is likely to be associated with the duration of the post-fledging care, the adaptive timing decisions of fitting multiple broods into a season of limited duration may play an important role in maximising the annual reproductive output.

Here, we analyse whether parent barn swallows (*Hirundo rustica* L.) adjust the duration of post-fledging care relative to factors associated with future reproductive attempts. As a facultative double-brooded species with low breeding synchrony the barn swallow provides the opportunity to investigate the adaptive decisions of time allocation to the different broods within the season. In particular, we test (1) whether the duration of post-fledging care is reduced in broods of renesting pairs compared to terminal broods, (2) whether the duration of post-fledging care is affected by the timing of the first breeding attempt of the season, and (3) whether the duration of post-fledging care is associated with individual variation in parental competence, as estimated by their tail streamer length. Further, we compare post-fledging feeding rates to patterns of parental time investment.

Materials and Methods

Study area and breeding parameters

The study was carried out in 2000 and 2002–2004 in a farmland area of approx. 20 km^2 near Lucerne, Switzerland (47°10’ N, 8°02’ E). Barn swallow nests at 60 farms were visited weekly from April to September and all clutches recorded. Towards the end of the incubation period, we inspected nests daily to record the exact hatching date (date, when the first egg of a brood hatched = day 1 of the nestling period). Nestlings were visited regularly until fledging. Fledging date of a brood was the day of the first nest departure. Fledging dates of first broods were considered to be a measure of the length of the remaining breeding season. In all pairs we recorded whether they started a subsequent breeding attempt or not. This was possible

because we caught and marked the adults of nearly all pairs during their first breeding attempt. Renesting pairs used the same or a nearby nest within the same farm.

The barn swallow (*Hirundo rustica* L.) is a small, insectivorous, socially monogamous, long-distant migrating passerine. Barn swallows arrive at their breeding sites in April and the breeding season lasts to mid September. In central Europe, 62–92 % of pairs are double-brooded (Møller 1984; Banbura & Zielinski 1998; Turner 2006). Clutches commonly have 4–6 eggs. Nestlings hatch approximately 15 days after the start of incubation. Nestlings are fed by both parents and fledge at 20–26 days of age. Increased annual parentage is acquired mainly by extra-pair copulations rather than by remating with a new partner (Møller 1988; Møller & Tegelström 1997), and exclusive post-fledging care of one sex generally does not occur. Consequently, post-fledging care is normally terminated simultaneously by both sexes and, if a subsequent brood occurs, the same individuals remate (De Lope & Møller 1993; M. Grüebler & B. Naef-Daenzer, unpublished data), probably because mate replacement is costly in multi-brooded species (Veiga 1996).

Post-fledging care

The duration of post-fledging parental care (DPC) was recorded using radio-telemetry. We caught 560 nestlings in 132 families before fledging at their nest during the night of day 19 or 20. To prevent premature departure, nest cups were closed using a flexible plastic cover. It was removed in complete darkness when the chicks had relaxed 5–10 min after they had been put back into their nest. 538 chicks were radio-tagged with a miniature transmitter of own construction (Naef-Daenzer 1993; Naef-Daenzer *et al.* 2005). Radio-tags (including battery) had a mass of 650 –750 mg, equivalent to 3.8 – 4.4 % of minimal fledgling mass (17 g). The aerial consisted of 10 cm of 0.15 mm multistrand steel. Tags operated for 3–5 weeks at a range of 2 to 5 km. Transmitters were attached using a Rappole-type harness made from 0.5 mm elastic cord (Rappole & Tipton 1990). A pilot study in 2000 did not reveal any measurable differences in behaviour, flight activity, and manoeuvrability or in survival between radio-tagged juveniles and a control group of colour-marked but untagged fledglings. For a further test of possible adverse effects of radio-tagging juvenile birds see also (Naef-Daenzer, Widmer & Nuber 2001b).

Each family was located twice per day and observed during a one-hour session, which included visual identification of all fledglings and recording of feeding rates as an estimate of the intensity of post-fledging care. Duration of post-fledging parental care (DPC) was defined

as the period from fledging to the last observed food delivery to the fledglings. Nine broods of triple-brooded pairs were excluded from analysis, as were nine broods that did not survive until family break-up. Overall, the DPC of 14 single, 51 first, and 49 second broods (total: 114 broods containing 494 individuals) of 88 pairs entered the analyses.

Parental traits

Parent birds were caught at night when their broods were 5 to 15 days old. We managed to catch 98.3 % of adults at least once and missed only three (1 male, 2 females). Adult birds were ringed and the length of the two outermost tail feathers (tail streamers) was measured with an accuracy of 0.5 mm. The average of the two measurements was used in the analysis.

Offspring condition and food supply

To test whether the value of the current brood was associated with the predictors and whether it could confound the results, we considered measures of offspring condition and post-fledging food supply in the analyses. Nestlings were measured when radio-tagged close to fledging on day 19–20. Body mass was taken to the nearest 0.5 g and length of the third outermost primary feather was measured to the nearest 0.5 mm. We analysed family means of mass and primary length. To obtain an index of daily supply of flying insects, we used the method of Grüebler & Naef-Daenzer (2007). Using binoculars, we counted flying insects passing a volume of approx. 1 m^3 air in front of white boards. By correlating daily mean counts with meteorological variables we built a model that allowed the daily food supply to be estimated from meteorological data. Here, we use predicted daily insect densities to account for variation in food supply. An index of food supply during the post-fledging period was determined by averaging the 10 daily supply indices from fledging to day 10 post-fledging.

Data analysis

The data had a hierarchical structure with broods nested within pairs. We included this hierarchical term as a random factor into a linear mixed model with restricted maximum-likelihood (REML) estimation of the associated variance component (Patterson & Thompson 1971) using Genstat 5, release 9.1 (Payne *et al.* 1993). Additionally, we controlled for between-year effects by incorporating year as an additive random effect of the year. As a control variable, we included the family size at day 8 post-fledging in the fixed model. Possible effects of family size will be published and discussed elsewhere. Further, the fixed

model included the factors “renesting” (parents start a subsequent brood or not) and “brood order” (first or second) and of three continuous covariates (fledging date of first brood, tail streamer lengths of both male and female). To account for possible non-linear effects, we included a second-order polynomial for the covariates. All two-way interactions between fixed factors and covariates (except interactions with family size) were incorporated in the analysis. Fixed effects were tested with the Wald test (Dobson 1990). For selection of fixed effects we used a stepwise backwards elimination procedure to identify the factors with a significant effect. At each step, the factor with the lowest Wald statistic was dropped from the model until only factors with $p < 0.05$ remained. We acknowledge that as in every step-wise variable selection, we used p values informally to point at the least ‘conspicuous’ factors and eliminate them. We do not claim that the p-values of the final model are correct. Post-fledging feeding rates were analysed accordingly. The random model included additive effects of year, and pair, as well as brood within pair and observation session nested within brood within pair. We used the same fixed effects and added (1) a second and third order polynomial of the age of fledglings (days after fledging), since parental feeding rates declined non-linearly with the chicks’ age, and (2) family size at the moment of the observation session. Analysis of feeding rates was restricted to the first 10 days post-fledging and only sessions of at least 50 minutes of continued observations were used. As offspring condition and food supply in the post-fledging period might be associated with the predictors, we tested for relationships between these possible confounding variables and the predictors in the analyses of investment by linear mixed models.

Results

Average observed DPC was 11.5 days ± 3.2 SD (n = 114; range: 6–24 days, Fig. 1), which was half as long as the duration of the nestling period (22.1 days ± 1.3 SD; n = 114; range: 20–27 days). Variation of DPC among broods was much larger than the variation of the nestling period. DPC was not related to the length of the nestling period ($r = -0.095$; n = 114, $P = 0.314$), even if we included the duration of the nestling period as a fixed effect in the mixed model (Wald statistic = 1.48; df = 1, $P = 0.224$).

After stepwise backwards elimination, four variables with significant effects on DPC remained (including family size, Table 1). The occurrence of a subsequent brood (referred to as “renesting”) reduced DPC by 3.8 days ± 0.5 SE. Thus, the DPC of double-brooded pairs in their first brood was significantly reduced. However, DPC did not differ between broods of

single-brooded pairs and second broods of double-brooded pairs (Table 1, Fig. 2). The estimated value of DPC, holding other significant variables (Table 1) at their means, for pairs without renesting was 13.2 days (± 0.4 SE), whereas for pairs conducting a subsequent breeding attempt it was 9.4 days (± 0.3 SE), i.e. a reduction of 29 %. Moreover, DPC was associated with the pair's timing of breeding, represented by the fledging date of the first brood in the season. The effect was non-linear and affected single, first and second broods, since the interactions "timing*renesting" and "timing*brood order" (first or second) showed no significant effect (Table 1, Fig. 3). Thus, double-brooded pairs consistently adjusted their DPC in both first and second broods to their timing of breeding. Timing (and therefore the length of the remaining breeding season) was mainly relevant in late pairs, in which DPC was considerably reduced (Fig. 3).

Female tail feather length (mean = 89.5 mm ± 5.2 SD; range: 78.7–106.0 mm) was negatively correlated with the timing of the pair ($r = -0.47$, $n = 86$, $P < 0.001$), and it had an additional negative effect on DPC. Pairs with a long-tailed female cared for a shorter period for their fledglings than did pairs with a short-tailed female (Table 1, Fig. 3). In contrast, male tail streamer length (mean value: 107.4 mm ± 8.6 SD; range: 86.0 mm to 140.3 mm) was not related to the pair's DPC (Wald statistic = 0.02; $P = 0.891$). Male and female tail feather lengths were not correlated ($r = 0.044$; $n = 87$, $P = 0.68$).

Feeding rates were negatively related to the age of fledglings and declined in a non-linear third order polynomial relationship (Table 2, Fig. 4). In accordance with the results on DPC, single-brooded pairs showed a different pattern of feeding behaviour compared to renesting birds. In the first 5 days after fledging, when feeding rates increased, there were no differences in the feeding rates between single-brooded and double-brooded pairs. From day 6 onwards, renesting pairs supplied a decreasingly smaller proportion of feedings. Thus, renesting pairs reduced both the duration and intensity of care. In contrast to the results on DPC, the feeding rates in second broods were higher than in first and single broods, as indicated by the significant effect of brood order (Table 2, Fig. 4). Further, the significant interaction between female tail length and fledgling age denotes that feeding rates of pairs with long-tailed females declined at an earlier age of the offspring. Neither the timing of the first brood, nor the brood size affected the feeding rates.

The offspring's fledging condition, as estimated by primary length and body mass (family means), did not differ between first and single broods, nor between first and second broods (primary length: renesting: Wald = 0.51, $P = 0.48$; brood order: Wald = 0.04, $P = 0.85$;

body mass: renesting: Wald = 2.09, P = 0.15; brood order: Wald = 0.17, P = 0.68). Offspring body condition was neither related to the timing of the first brood (primary length: timing: Wald = 0.04, P = 0.85; timing^2: Wald = 0.10, P = 0.75; body mass: timing: Wald = 0.74, P = 0.39; timing^2: Wald = 0.62, P = 0.43) nor to the female tail feather length (primary length: Wald = 1.89, P = 0.17; body mass: Wald = 2.73, P = 0.10). Moreover, the food supply during the post-fledging period was not associated with the timing of the first brood (timing: Wald = 1.07, P = 0.30; timing^2: Wald = 0.67, P = 0.41) nor with the female tail feather length (Wald = 1.41, P = 0.24), and it did not differ between first broods and single broods (renesting: Wald = 0.37, P = 0.55). However, food supply was significantly decreased in second broods compared to first and single broods (brood order: effect = -8.73 ± 1.83 insects m^{-3} $(3\ min)^{-1}$, Wald = 22.87, P < 0.001).

Discussion

Our results show that barn swallows adjust the duration of post-fledging care according to their seasonal breeding strategy. In particular, breeding pairs reduced the period of post-fledging care (1) if they renested within the same season, (2) if their start of breeding in the season was late, and (3) if female condition (as estimated by the length of the outermost tail feathers) was high. The pattern in post-fledging feeding rates matched with these adjustments in time investment, except that parents fed second broods more often than first broods.

These results are in agreement with the hypothesis of an intra-seasonal trade-off in the allocation of time between successive broods, and suggest that double-brooded pairs reduced the time investment in their first brood in favour of an earlier start of the second brood. We therefore suggest that time is an important currency of parental investment in multi-brooded species. Estimation of the total post-fledging investment considering differences in the duration and in the intensity of post-fledging food provisioning revealed that the parental investment into first broods was 68 % of the investment into single broods. Due to higher feeding rates, investment into second broods was 133 % of the investment into single broods. Thus, double-brooded pairs invested nearly twice as much post-fledging effort into their second brood than into their first. Earlier studies on multi-brooded species observed prolonged post-fledging investment in terminal broods and proposed a trade-off between successive broods (Kluyver *et al.* 1977; Edwards 1985; Verhulst *et al.* 1997). However, we are not aware of any study quantifying the post-fledging investment to the different broods in relation to future reproductive attempts, timing and parental competence.

The proposed trade-off in the allocation of efforts between successive broods assumes that post-fledging investment in a particular brood, including its duration, is part of an optimising process. This implies that reducing post-fledging care is costly. The rare studies on the fitness relevance of the timing of family break-up in altricial birds give evidence that early termination of care indeed reduces offspring survival or future fecundity (Verhulst *et al.* 1997; Cam, Monnat & Hines 2003). These costs should be outweighed by benefits of an early start of the subsequent brood. Date-related decline in fledging condition and recruitment was found in various seasonally breeding passerines (e.g. Verhulst, van Balen & Tinbergen 1995; Svensson 1997; Nilsson 1999; Naef-Daenzer *et al.* 2001a).

The food supply in the post-fledging period of second broods (i.e. in the late season) was considerably reduced. Nevertheless, feeding rates in second broods were higher than in first broods. This does not necessarily indicate that second broods received more food, as the size of each meal decreases during the season and fewer daylight hours are available for feeding (Waugh 1978; Jones 1987; Turner 2006). However, the increased feeding rates in second broods are likely to be a good estimate of the parents' effort. Hence, differences in environmental conditions affect the intensity, but not the duration of parental post-fledging investment in barn swallows.

The duration of post-fledging investment depended on the pairs' timing of the first brood in the season. Late double-breeders abandoned the fledglings of their first and second brood after a shorter care period compared to early pairs. Late breeding pairs may experience additional trade-offs between post-fledging care of second brood chicks and preparation for migration including moult (Evans Ogden & Stutchbury 1996; see also Arroyo, De Cornulier & Bretagnolle 2002). This is supported by three recent studies on barn swallows which suggest that an early end of reproduction is advantageous because the following body moult and migratory fattening are time consuming processes (Pilastro & Magnani 1997; Pérez-Tris *et al.* 2001; Rubolini, Massi & Spina 2002). Further, it is supposed that the environmental conditions underlying the decline in fledgling survival is non-linear, being steeper at the end of the season.

The results indicate that the post-fledging care period was also slightly reduced in early pairs. Early pairs have a higher chance to conduct a third brood in the season and the duration of post-fledging care might be the result of optimising the time allocation over three annual broods.

Our results further revealed that pairs with long-tailed females provide shorter post-fledging care. This indicates that factors associated with female tail length affected the time investment to the broods. Long tails in female barn swallows are viewed as a morphological trait indicating high body condition (Møller 1993). Therefore we suggest that the high body condition and physiological competence of long-tailed females allow optimising their breeding strategy by reducing the duration of post-fledging care. Long-tailed females have been shown to arrive earlier (Cuervo, de Lope & Møller 1996), to have more viable chicks (Møller 1994) and to survive better to the next breeding season (Møller & Szep 2002). These effects possibly affect the optimal time allocation to the broods.

Tail feather length of males, which is negatively associated with the male investment in terms of food provided to nestlings (De Lope & Møller 1993), was not related to the duration of post-fledging care. This suggests that the termination of care in barn swallows is under female control. Studies of Verhulst (1998) and Rubolini *et al.* (2002) showing that females, but not males incur between-season costs of increased time investment, are in line with this.

In conclusion, this study represents an important step to the understanding of intra-seasonal trade-offs in the allocation of time. That parental post-fledging investment differs greatly between single, first and second broods of double-brooded species is new and reveals that the extent and duration of post-fledging parental care are important traits of the breeding strategy. Adjustments of the duration of care according to future reproduction and according to the timing of breeding occurred only after the brood had left the nest. Therefore, we suggest that future research on differential parental investment and its costs and benefits must focus on the post-fledging period.

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Table 1. Results of the linear mixed model analysis with REML estimation of variance components of factors affecting the duration of post-fledging parental care (DPC; N = 114; random effects: pair, brood nested within pairs, and year). Only significant fixed effects are shown. Non-significant variables and interactions were eliminated in a backward procedure, at each step dropping the factor with the lowest Wald statistic with $p > 0.05$ from the model. The effect size of the factor "renesting" is given for broods followed by a subsequent brood (versus broods without subsequent renesting). Effects ± SE and Wald statistics are given with their significance levels. Degrees of freedom for all variables = 1.

Variables[1)]	Effect ± SE[2)]	Wald statistic	P
Timing	0.569 ± 0.220	6.97	0.008
$(\text{Timing})^2$	-0.003 ± 0.001	6.70	0.010
Female tail	-0.112 ± 0.054	4.37	0.037
Renesting (yes, no)	-3.812 ± 0.509	56.10	<0.001

[1)] Family size at day 8 post-fledging: Wald statistics = 11.26, df = 1, $p < 0.001$
[2)] Constant: 13.23 ± 0.34

Table 2. Results of the linear mixed model analysis with REML estimation of variance components of factors affecting the post-fledging feeding rates (feedings per fledgling per hour; N = 1225 observation sessions on 84 families; post-fledging age of juveniles ≤ 10 days). Sessions lasting at least 50 minutes were used. The random model contained the random effects "pair", "year", "broods within pairs", and "session within broods within pairs". Only significant fixed effects remaining after a backward elimination procedure are shown. Effect sizes of the factor "renesting" and the interaction "renesting*age" are given for broods followed by a subsequent brood (versus broods without subsequent renesting). Effects ± SE and Wald statistics are given with their significance levels in the final model. Degrees of freedom for all variables were 1.

Variables	Effect ± SE[1)]	Wald statistic	P
Renesting	-1.311 ± 0.72	24.13	<0.001
Renesting*age	-0.403 ± 0.11	16.06	<0.001
Brood order	1.529 ± 0.72	4.54	0.033
Age	2.634 ± 0.66	65.07	<0.001
$(Age)^2$	-0.410 ± 0.14	61.54	<0.001
$(Age)^3$	0.015 ± 0.01	4.56	0.033
Female tail	0.004 ± 0.05	0.00	0.951
Female tail*age	-0.025 ± 0.01	5.95	0.015

[1)] Constant: 6.575 ± 0.90

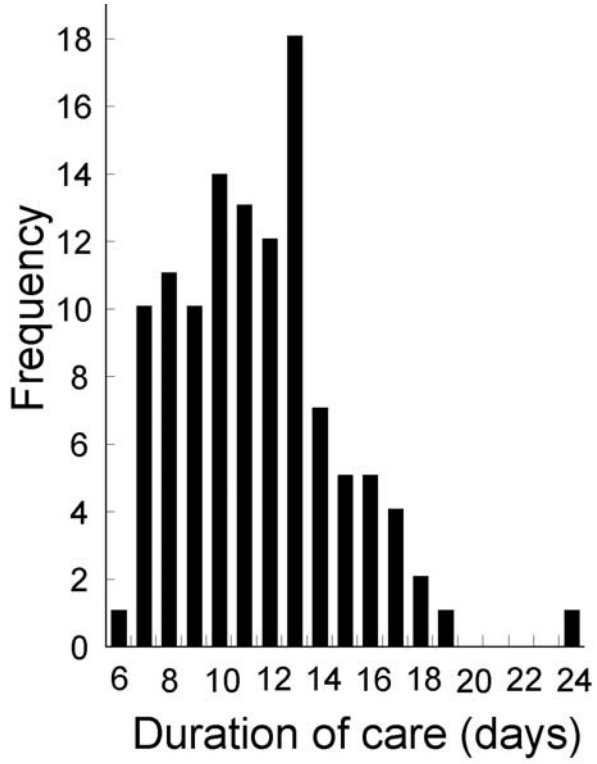

Fig. 1. Frequency distribution of the duration of post-fledging care in days (N = 114 broods), defined as the period from fledging of the first juvenile in a brood to the last observed parental food delivery to any of the fledglings. Broods were excluded if fledglings did not survive to independence. Broods of the same pair were included (N = 88 pairs).

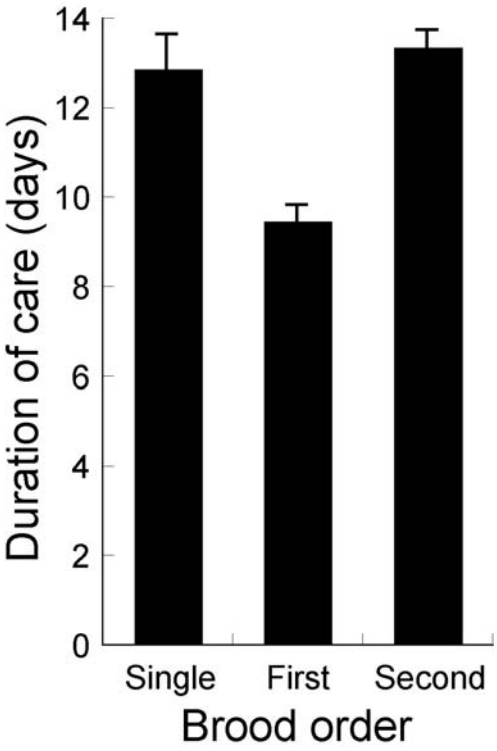

Fig. 2. Effect of renesting on the duration of post-fledging care (DPC). Predicted values of DPC (days ± SE) for 14 single, 51 first and 49 second broods of 88 pairs are shown (total: 114 broods containing 494 individuals). The model of Table 1 with an additional effect of "Brood order" was used to build the figure. Other significant variables (see Table 1) were kept constant at their means.

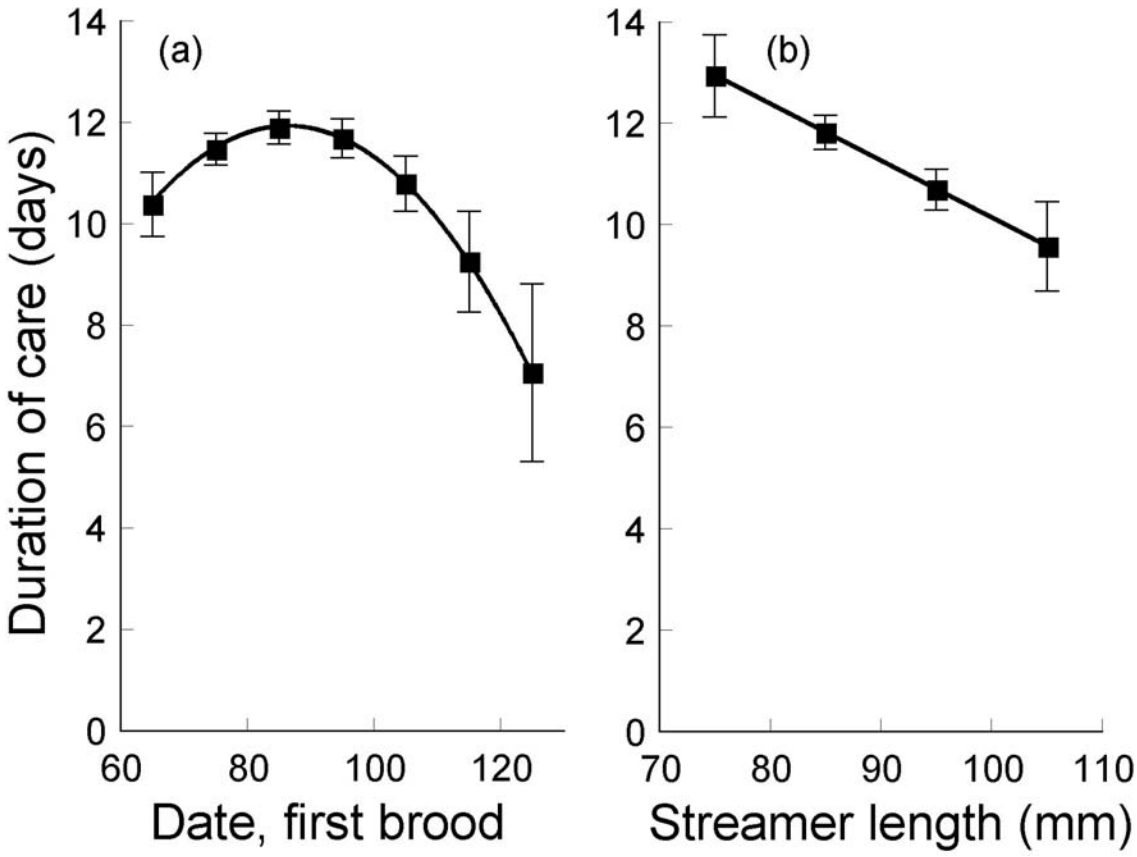

Fig. 3. Effects of (a) the timing of the first brood in the season, and (b) female tail streamer length (mm) on the duration of post-fledging care (DPC). Predicted values of DPC (days ± SE) are shown. Date 1 = 1 April. Other significant variables (see Table 1) were kept constant at their means.

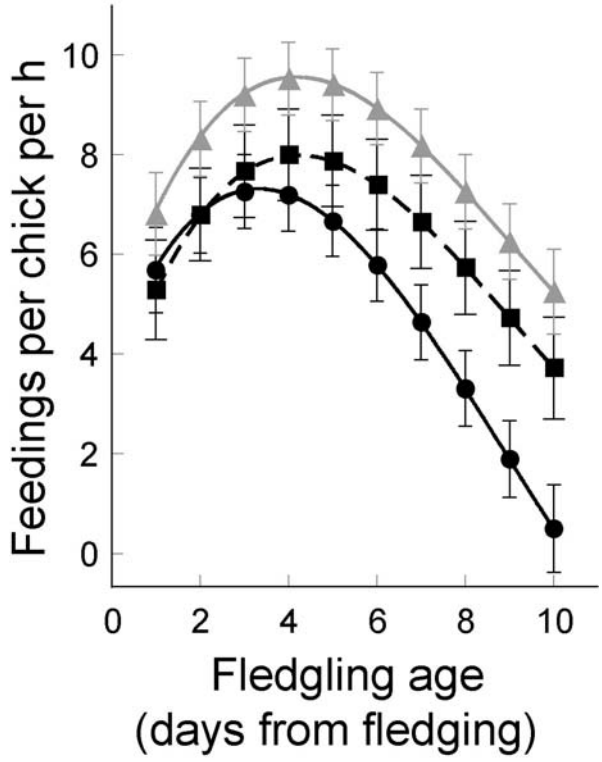

Fig. 4. Daily post-fledging feeding rates of single broods (black squares, broken line), first broods (black dots, solid line) and second broods (grey triangles, solid line). Predicted values (feedings per chick per hour ± SE) in relation to fledgling age (days since fledging) are shown. Feeding data were restricted to fledgling age ≤ 10 days. Other significant variables (see Table 2) were kept constant at their means.

SYNTHESIS

The present thesis in the field of behavioural ecology and life-history evolution investigates the reproductive system of the barn swallow, in particular behavioural mechanisms and selective processes operating in the post-fledging period. This model species offered a multi-brood reproductive system in a seasonal environment with excellent opportunities for experimentation.

Exploring differential survival in relation to variance in life-history traits is a direct approach to establish evidence for evolutionary processes and to get insight into the ecological mechanisms driving them. In the example species, the fitness consequences of differential timing and differential parental investment emerged only after the juvenile birds had left the nest. The experimental and observational evidence from the post-fledging period improves the understanding of the proximate mechanisms maximising the annual reproductive output.

Initially, I hypothesised that parent barn swallows face an intra-seasonal trade-off in the time allocation between successive broods, and I formulated three predictions out of this general hypothesis: (1) A late start of second broods is costly in terms of reduced juvenile survival, (2) early termination of care of first broods is costly in terms of reduced juvenile survival, and (3) pairs conducting a second brood reduce the duration of care of first brood fledglings. The results of my thesis are consistent with all three predictions. Thus, I conclude that barn swallows face a strong intra-seasonal trade-off in the allocation of their efforts to their broods: Parent barn swallows sacrifice a part of the output of their first brood by a short post-fledging investment thereby increasing the output of the subsequent breeding attempt by an earlier start.

Life history theory predicts that double-brooded barn swallow pairs optimise the allocation of time to yield a net gain in the annual reproductive output compared to single-brooded pairs. Figure 1 represents estimates of the total annual reproductive output for the double-brooded and the single-brooded breeding strategy in relation to the timing of reproduction. It combines the results of this thesis with data on the seasonal variation of brood size and interclutch-interval in the study population. The figure illustrates some of the main implications of this thesis as discussed below.

The output of the first brood of double-brooded pairs (Fig. 1, broken line) is reduced by approximately 0.8 chicks compared to single-brooded pairs. This reduction is causally related to the shortened duration of post-fledging care in first broods, which in turn reduces the chicks' post-fledging survival (see chapter 4 and chapter 5). Hence, double-brooded pairs sacrifice c. 30 % of the output of the first brood in favour of an early start of their second breeding attempt. In fact, this strategy yields a net gain since the seasonal reproductive output of double-brooded pairs exceeds that of parents breeding once (Figure 1, solid line). I conclude that time is an important currency of investment in the breeding system of barn swallows. The results suggest that the observed allocation of time to the breeding attempts is close to the optimum, thereby maximising the annual reproductive output.

Early breeding pairs have the highest annual reproductive output. In early breeders, the double-brood strategy yields nearly twice as many surviving offspring as pairs breeding late and only once. The quantitative models for the different strategies explain the importance of early arrival and quick mating in the breeding system of barn swallows (Møller 1994a; Møller 1994b; Møller et al. 2003; Møller et al. 2004; Ninni et al. 2004). The large difference between the two alternative strategies would have been overlooked when focusing only on the pre-fledging period.

The contribution of second broods to the annual reproductive output declines steeply in the course of the season. In early pairs, the second brood may even contribute more to the annual output than the first. The break-even point where the double-brood and the single-brood strategy yield equal reproductive output is on a laying date of 5 June (first clutch, Fig. 1). The over-all output of the two strategies and the break-even date strongly depend on the slope of the decline in the productivity of the second brood. I therefore suggest that factors affecting the extent and pattern of this decline are of crucial importance for the individual reproductive output and thus, for the evolution of the characteristics of the reproductive system. In chapter 3, I showed that the seasonal decline in post-fledging survival varies annually causing annually varying payoffs of different strategies. This leads to two broader implications: First, barn swallows arrive later and depart earlier at higher latitudes and they also arrive later at higher altitudes (Huin et al. 1998; Sparks et al. 2001; Turner 2006). Consequently, barn swallow populations at higher latitudes and altitudes are faced with shorter breeding seasons. These differences suggest that populations should differ in the optimal solution of the present trade-off in the allocation of time according to the length of the breeding season and the

seasonal pattern of environmental conditions. Second, the fitness relevance of the timing decisions is of interest with respect to global climate change. In temperate zones, the conditions favouring successful avian breeding have been advanced and prolonged in the past decades (Menzel et al. 1999; Cook et al. 2005) and there is evidence for shifts in avian life-history parameters and in population dynamics (Saether et al. 2000; Møller 2002; Visser et al. 2003; Both et al. 2005; Gordo et al. 2005). The results of this thesis suggest that in barn swallows an extended breeding season results in a higher contribution of the second brood to the annual output. Climate change therefore is supposed to favour a multi-brooded strategy in barn swallows.

The average post-fledging survival in the first three weeks after leaving the nest was 0.45. This suggests that juvenile mortality after this critical period is not substantially higher than that of adults. I conclude that the first weeks of the post-fledging period are a main bottleneck in the life of juvenile barn swallows. Similar patterns in juvenile mortality have been shown for other species (e.g. great tits: Naef-Daenzer et al. 2001; ovenbirds: King et al. 2006), which suggests that the post-fledging period is an important time in the life of altricial birds in general.

The general hypothesis of a trade-off in the time allocation between successive broods assumes that there is no overlap between the two broods. Thus, it ignores an important temporal characteristic of multi-brooded reproductive systems (e.g. Edwards 1985). Overlapping the broods would be an optimal strategy to enhance the survival prospects of both the preceding and the subsequent brood (Burley 1980; Smith et al. 1989). In our study population, if present, brood overlap is normally very short (18 % of pairs showed at least a small overlap between successive broods of 3.4 ± 2.3 SD days), but 5.6 % of pairs with known duration of post-fledging care prolonged the overlap beyond the egg laying period of the subsequent clutch, presuming an overlapping strategy. Therefore, I suggest that overlapping broods usually induces higher costs than delaying the subsequent brood. These costs might be associated with the fact that in barn swallows extra-pair copulations are frequent (Møller 1988; Møller et al. 1997) and therefore males might benefit from mate guarding rather than from continuing post-fledging care when females are laying the next clutch.

In conclusion, this thesis demonstrates that extending investigations of avian reproductive systems beyond fledging reveals exciting new insights into life history evolution and behavioural ecology, even of well-known example species. Hence, the study contributes to understanding reproductive systems as well as the evolutionary processes shaping them. Future research on the ecology and evolution of altricial birds should address the mechanisms operating in the period between fledging and first breeding.

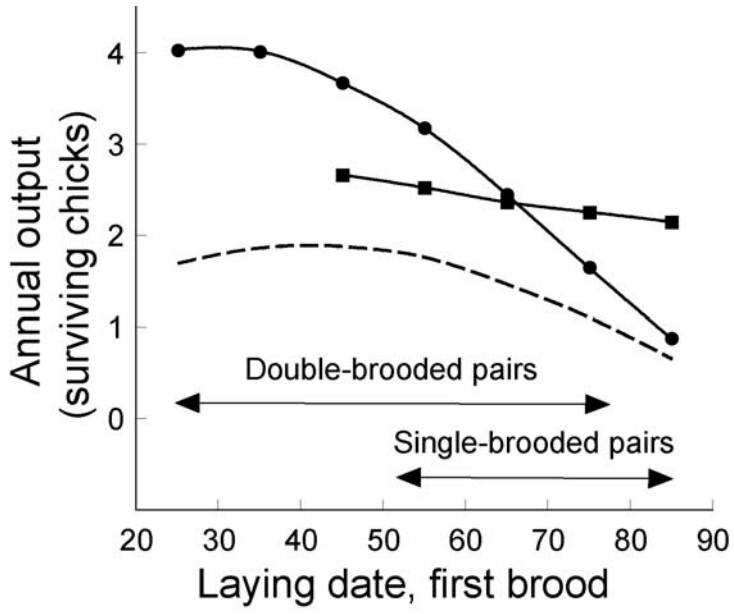

Fig. 1. Annual reproductive output (number of chicks surviving three weeks after leaving the nest) in relation to the laying date of the first annual clutch. The annual output for double-brooded pairs (circles) and single-brooded pairs (squares) are shown. Additionally, the reproductive output of the first brood of double-brooded pairs (broken line) is illustrated. This figure is based (1) on experiments and observational results on the seasonal variation of post-fledging parental care and its effect on post-fledging survival, (2) on experimental and observational results on the seasonal decline in the post-fledging survival of second broods, (3) on the seasonal variation in the brood size of first and second broods in the study population (seasonally decreasing), and (4) on the seasonal variation of the interclutch-interval in the study population (seasonally increasing). Laying date: 1 = 1 April.

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